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LOW TEMPERATURE EFFECTS ON THE FLOWERING OF *CHRYSANTHEMUM MORIFOLIUM* RAMAT

By DAPHNE VINCE
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POST (1939) reported that flowering in glasshouse chrysanthemums was retarded or prevented when the night temperature was 50°F. or below during short-day induction and (1942) recommended a night temperature of 60°F. during this period. Recently Samman (1958) has stressed the importance of temperature during the early part of the short-day period ; low temperatures during the initial short days may cause multiple crown formation and delay flowering, the magnitude of the effect depending on their degree and duration. Low temperature given immediately preceding short days, or following ten short days at 60°F., caused little delay in flowering. Cathey (1954a, 1955) investigated the effects of a wide range of temperatures given at different stages of growth. Considerable variations in response occurred : certain varieties (termed " thermo-positive ") showed a marked delay in flowering when low temperatures were given during short days, others (" thermo-negative ") were delayed by high temperature during flower development, and a third group (" thermo-zero ") was largely insensitive to temperature. Cathey (1954b) also found that a low night temperature was more effective in causing delay than a low day temperature.

The importance of low temperature as a factor retarding flowering in glasshouse chrysanthemums is thus well established. However, the American investigations have considered mainly spray varieties and have largely been concerned with overall delays in flowering time and effects on spray type and peduncle length. No studies appear to have been made on English " standard " (i.e. disbudded) varieties, and this investigation was undertaken to determine the influence of temperature on flowering time, flower type and quality, and extent of the variation in varietal behaviour.

METHODS.

The experimental conditions made it possible to control night temperatures only. Accordingly the temperatures given refer to conditions between 4 p.m. and 8 a.m. ; temperatures during the day were higher and varied with the time of year. During the day, all treatments were randomized in the same glasshouse compartment ; at night, treatments were given in controlled environment rooms where positional effects were small.

The long-day treatments (except in Experiment 1) consisted of 8 hours of daylight with 9 hours of supplementary low intensity light from tungsten-filament lamps ; short photo-periods consisted of 8 hours of daylight.

In Experiments 2, 3 and 4, all, or many, of the plants in some treatments failed to reach anthesis ; because of this, statistical treatment of these data on time of

flowering has not been attempted. Where some plants in a treatment failed to flower, the number of days to anthesis for these plants was taken arbitrarily as the number of short days received up to the end of the experiment ; as a result, the delay in flowering is underestimated for these treatments. The number of plants which failed to flower is given in each case.

RESULTS.

Effect of low night temperature during short-day induction (exp. 1).

Since low temperature during short days has been reported to be particularly effective in delaying flowering, its influence was investigated for a range of English varieties. Cuttings of seven varieties (listed in Table I) were potted on 22nd and 23rd March 1955 and grown in long photo-periods (natural day-length supplemented with tungsten-filament lamps to give a total of 17 hours) at 60°F. (15·5°C.) night temperature. On 20th May the plants were transferred to short-day conditions and the following temperature treatments begun :

60°F. night temperature throughout,
60°F. night temperature until bud visible macroscopically, then 50°F. (10°C.),
50°F. night temperature until bud visible, then 60°F.,
50°F. night temperature throughout.

Two lateral shoots were allowed to develop on each plant after cutting back on 30th April ; three replicate plants of each variety were grown in each temperature treatment.

Date of anthesis.

Although the absolute delay in flowering time was not very great, the results (Table I) indicate the existence of two stages of development with regard to sensitivity to low night temperature during short days. Low temperature given until the bud was visible delayed flowering ; varieties, however, differed in their response and only Imperial Pink and Finale were markedly delayed. When given after the bud became visible, low night temperature did not delay flowering.

Leaf numbers did not differ as a result of the temperature treatments, thus indicating a slowing of the rate of bud development at low temperature rather than a delay in initiation.

Flower quality.

Table II shows clearly that flower diameter was increased by exposure to 50°F. after the bud was visible. The night temperature from the beginning of the short-day treatment until the bud was visible had little effect on flower size.

Differences in numbers of ray florets as a result of the temperature treatments were small and non-significant. Consequently the increased flower size at the lower temperature must have resulted from an increase in floret length.

Flowers developing at a night temperature of 60°F. were paler in colour, especially in bronze and pink varieties, as well as smaller than at 50°F. ; centres expanded more slowly and, in reflexed varieties, the outer florets failed to reflex. In American Beauty the centre florets failed entirely to expand at 60°F. and the centre of the flower remained flat instead of developing the normal globular form.

TABLE I.

Effect of night temperature during short-day induction on the date of anthesis.

Night temperature (°F.)		Days to anthesis from start of short days							Mean, all varieties
Until bud visible	After bud visible	American Beauty	Balcombe Perfection	Crensa	Finale	Imperial Pink	Mayford Crimson	Rose Harrison	
60(15·5°C.)	60	(89·0*)	78·3	73·0	88·7	89·7	74·0	95·3	84·1
60	50	88·3	72·0	75·0	89·0	90·0	73·0	89·0	82·3
50(10°C.)	60	(92·0*)	79·3	76·7	111·7	104·3	80·0	101·0	92·1
50	50	95·7	79·0	76·0	115·7	103·3	76·7	103·3	92·1
Significant difference at P=0·05		3·06							1·20

Main effects : temperature until bud visible, P<0·001 ; temperature after bud visible, non-significant.
* Centre florets remained unexpanded and figures refer to expansion of outer ring of florets only.

TABLE II.

Effect of night temperature during short-day induction on flower diameter.

Night temperature (°F.)		Mean flower diameter (cm.)							
Until bud visible	After bud visible	American Beauty	Balcombe Perfection	Crensa	Finale	Imperial Pink	Mayford Crimson	Rose Harrison	Mean, all varieties
60(15·5°C.)	60	8·0	8·7	8·6	7·3	7·6	8·6	7·2	8·0
60	50	8·9	9·6	10·1	9·1	8·9	11·0	9·5	9·6
50(10°C.)	60	7·4	9·0	9·4	7·2	7·3	9·3	8·2	8·3
50	50	8·2	11·1	10·7	8·7	9·0	11·5	9·3	9·8
Significant difference at P=0·05		0·84							0·31

Main effects ; temperature until bud visible, P=0·05 ; temperature after bud visible, P<0·001.

TABLE III.

Effect of low night temperature at different stages of growth.

Night temperature (°F.)			Days to anthesis from beginning of short days			Number of leaves to bud		
During long days	During short days		Balcombe Perfection	Crensa	Mayford Crimson	Balcombe Perfection	Crensa	Mayford Crimson
	Until bud visible	After bud visible						
60	60	60	88·0	148·0	89·3	26·0	36·0	24·0
60	60	50	90·3	156·7	91·9	29·7	40·7	23·0
60	60	40	108·0+	132·3	102·3	29·0	32·3	22·3
60	60	60*	88·0	148·0	89·3	26·0	36·0	24·0
60	50	60	149·0	249·3	186·8	41·7	59·0	57·5
60	40	60	260·0	F	F	55·6	56·7	87·8
60(15·5°C.)	60	60*	88·0	148·0	89·3	26·0	36·0	24·0
50(10°C.)	60	60	94·5	166·0	120·0	28·8	38·7	33·3
40(4·5°C.)	60	60	148·3	188·3	131·8	38·0	42·0	36·3
60	60	60*	88·0	148·0	89·3	26·0	42·8	24·0
50	50	50	184·8	246·5	194·3	46·8	57·3	57·3
40	40	40	273·8	F	F	61·0	59·8	76·3
Significant difference at P=0·05						11·33	7·05	7·61

* Data repeated for ease of comparison.
\+ One plant only.
F, Plants failed to reach anthesis.

EFFECT OF LOW NIGHT TEMPERATURE AT DIFFERENT STAGES OF GROWTH (EXP. 2).

In this experiment a wider range of temperature treatments was used with a smaller number of varieties. Three different night temperatures, 60-63°F., 50-53°F. and 40-43°F. were used : (1) during long days, (2) from the commencement of short days until the bud was visible, (3) from bud visibility until anthesis.

Rooted cuttings were cut back on 10th October 1955 and one lateral only was allowed to develop on each plant. Four replicate plants of each of three varieties were grown in each temperature treatment. Temperature and day-length treatments commenced on 10th October ; plants received long days for 5½ weeks and were transferred to short days on 18th November.

The experiment was discontinued in August 1956 ; by this time buds had formed in all treatments but many plants at 40°F. during short days had failed to reach anthesis.

Date of anthesis.

The absolute delay in flowering time was much greater than in the previous experiment and all three varieties behaved in essentially the same manner (Table III). The greatest delay occurred when low night temperatures were given during the short-day period until the buds became visible. All varieties formed buds at 40°F. but in Mayford Crimson and Crensa these failed to develop. At 50°F. all plants flowered but were considerably delayed; the increases in leaf number accompanying the delay in flowering were large.

Low night temperature given during the long-day period resulted in delayed flowering, even when plants were transferred to 60°F. in short days ; significant increases in leaf number accompanied the delay in Mayford Crimson and Balcombe Perfection, but not in Crensa.

As in the previous experiment, low temperatures after buds had become visible caused very little delay in the time of flowering.

Flower quality.

Flower quality was primarily determined by the night temperature at which the flower opened (Table IV). Maximum size and quality occurred in plants transferred to 50°F. following formation of the bud at 60°F., but flowers of good size and colour developed when plants received 50°F. throughout short days. Transfer to 40°F. (following bud formation at 60°F.), produced poorer blooms though of large size ; the colour was intense but the flowers were flatter than at 50°F. At 40°F. throughout short days, only the variety Balcombe Perfection produced flowers ; these were of poor quality and contained only a small number of rather broad ray florets.

EFFECT OF NIGHT TEMPERATURE ON DIFFERENT VARIETIES (EXP. 3).

The range of response to low night temperature of a number of English " standard " varieties was examined and, for comparison, one " thermo-positive " American spray variety Encore (Cathey, 1955) was grown. Since in the previous experiments the temperature after the buds became visible had little effect on the time of flowering, plants in all treatments were transferred to 50°F. when the buds became visible.

TABLE IV.

Effect of night temperature on flower diameter.

Night temperature during short days (°F.)		Mean flower diameter (cm.)			Mean, all varieties
Until bud visible	After bud visible	Balcombe Perfection	Crensa	Mayford Crimson	
60	60	8·2	8·7	9·2	8·7
60	50	10·1	10·1	12·0	10·7
60	40	10·2	9·6	12·1	10·6
60 (15·5°C.)	60	8·2	8·7	9·2	8·7
50 (10°C.)	60	8·1	8·0	8·8	8·3
40 (4·5°C.)	60	8·3	F	F	—
60	60	8·2	8·7	9·2	8·7
50	50	10·5	10·1	11·8	10·8
40	40	9·8	F	F	—
Significant difference at P=0·05					0·82

F, Plants failed to reach anthesis.

Rooted cuttings of 19 varieties were cut back on 11th September 1956 and the the following temperature treatments commenced :

60°F. night temperature throughout,
60°F. night temperature during long days, 50°F. during short days,
50°F. night temperature during long days, 60°F. during short days,
50°F. night temperature throughout.

Five replicate plants of each variety were grown and only one lateral shoot was allowed to develop on each plant. Long photo-periods were given for 6½ weeks from 11th September to 27th October, when the plants were transferred to short days. The experiment was discontinued on 8th July 1957, by which time all plants had formed buds.

Date of anthesis.

At 60°F. throughout, only 82% of the plants produced terminal flowers, suggesting that some factor other than temperature (probably low light intensity) was affecting flowering ; for most varieties the time taken to reach anthesis was longer than at 60°F. in the summer and early autumn (Mason and Vince, in press). Seven varieties, however, showed normal development of the terminal inflorescences of all plants at 60°F. and in three others one bud only failed to develop (Table V). The data from these ten varieties have been considered in the following discussion. In the remaining varieties more than one terminal inflorescence bud failed to develop or showed abnormally delayed development at 60°F. ; the comparison of this treatment with low temperature could not, therefore, validly be made and the data for these plants have not been considered. The varieties were Celebrity, Dora Ramsay, Late Delight, Loveliness, Magnet, Mayford Supreme, Finale, Snowcap, and Superlative.

The date of flowering of the terminal inflorescence only was recorded ; where this aborted and a lateral shoot flowered, the plant was considered to have failed to flower.

TABLE V.

Effect of low temperature during long and short days on date of flowering.

Variety		Night temp. °F.	Days to anthesis from beginning of the short-day treatment			
			In long days			
			60 (15·5°C.)	60	50 (10°C.)	50
			In short days			
			60	50	60	50
American Beauty	All plants at 60°F. throughout flowered		108	133	183	249+(3)
Balcombe Perfection			106	120	216+(3)	172
Encore			73	94	F	241+(2)
Friendly Rival			87	157+(1)	149	F
Fred Shoesmith			86	99	135	195+(2)
Gordon Wells			93	155	191+(2)	F
Rose Harrison			130	132	156	241+(3)
Crensa	One plant of each at 60°F. throughout failed to flower		149+(1)	191+(2)	181	256+(4)
Mayford Crimson			147+(1)	F	165	F
Worthing Success			190+(1)	255+(4)	194	F

F, All plants failed to reach anthesis.

+, Where some plants in a treatment failed to flower the number of days to anthesis was taken arbitrarily as 260, i.e. from the beginning of the S.D. treatment to the end of the experiment; the number of plants which failed to reach anthesis is given in brackets.

In all except Encore and Balcombe Perfection the greatest delay in flowering occurred when 50°F. was continued throughout.

In six varieties low temperature given during the long-day period delayed anthesis more than when given during the short-day period, even though the former continued for only 6½ weeks. Low temperature during long days resulted in delayed initiation, i.e. an increase in leaf number (Table VI), except in Balcombe Perfection, followed by delayed or suppressed floret initiation which in some cases resulted in abortion of the terminal inflorescence, as for example in Encore and Balcombe Perfection.

In four varieties low temperature given during short-day induction delayed flowering more than when given in long days ; except in Mayford Crimson (where anthesis failed) and Gordon Wells, leaf number was not affected and the effect of low temperature was mainly to delay floret initiation and development.

EFFECT OF TEMPERATURE AND LIGHT INTENSITY ON FLOWERING (EXP. 4).

In Experiment 1, which was carried out in the summer, low night temperatures caused only small delays in the time of flowering, whereas in Experiment 3 nine

TABLE VI.

Effect of low temperature during long and short days on increase in leaf number, as compared with 60°F. throughout whole period.

Variety	Night Temp. °F.	Leaf number to bud; increase compared with 60°F. throughout			
		In long days	60 (15·5°C.)	50	50
		In short days	50 (10°C.)	60	50
American Beauty			−1	21	28
Balcombe Perfection			−3	−5	−6
Encore			−1	9	23
Friendly Rival			0	13	59
Fred Shoesmith			−1	14	9
Gordon Wells			10	6	11
Rose Harrison			−8	5	4
Crensa			0	21	26
Mayford Crimson			35	5	33
Worthing Success			1	12	2
Mean, all varieties			3·2	10·1	18·9

varieties failed to develop normally at 60°F. throughout and flowering in all varieties was markedly delayed by low temperature. This latter experiment was carried out during the autumn and winter when the light intensity was low. Since low light intensity has been reported to be a factor delaying flowering (Watson and Andrews, 1953), the interaction of light intensity with temperature at different stages of growth was investigated in the following experiment. A further treatment was included to compare the effects of different day-lengths during short-day induction.

The following treatments were combined factorially, giving 64 treatments (Table VII) :

1. Night temperature during long days ; 60°F., 50°F.
2. Night temperature during short days ; 60°F., 50°F.
3. Light intensity during long days ; natural daylight, $\frac{1}{3}$ daylight (reduced with cheesecloth).
4. Light intensity during short days ; natural daylight, $\frac{1}{3}$ daylight.
5. Day-length during short days ; 8 hours, one week at 14 hours then 13 hours.

Rooted cuttings of Fred Shoesmith (yellow) and Balcombe Perfection were cut back on 11th September 1957 and one lateral shoot was allowed to develop on each plant ; five replicate plants of each variety were grown in each treatment. Treatments began on 12th September. Long days continued for six weeks until 25th October, when plants were transferred to short days. The differences in light intensity were maintained only during the eight hours in natural daylight ; the temperature differences, as before, were maintained only during the remaining sixteen hours from 4 p.m. to 8 a.m., when the plants were in darkness or receiving low intensity supplementary light.

The experiment was discontinued on 2nd May 1958, when the majority of the

plants had budded. In those plants which remained vegetative, the number of expanded leaves was counted on that date.

Date of anthesis.

The two varieties showed the same general type of response to the temperature and light-intensity treatments. Flowering was delayed by low night temperature (Table VII) given both during long and short days ; maximum delay occurred when 50°F. was continued throughout. Light intensity during long days had no effect on flowering date ; low light intensity during short days, however, resulted in a large delay in flowering and many plants had failed to reach anthesis by 2nd May.

During short-day induction, therefore, both low temperature and low light intensity caused large delays in flowering. Low light intensity during the period of vegetative growth in long days apparently had little effect on the time of flowering, provided that the plants were at high intensities during short-day induction. On the other hand, low night temperature during long days resulted in delayed flowering, even when plants were transferred to high temperatures at the beginning of short days. A number of these plants produced terminal inflorescence buds which failed to develop to anthesis. Fig. 1 illustrates the difference in behaviour of the terminal buds when plants were given low temperatures during long or short days.

Day-length during short days had no overall effect on the date of flowering ; however, if only the most favourable temperature (60°F.) and light intensity (high, or low followed by high) treatments in Table VII are considered, the longer day-length is found consistently to have delayed flowering by about 30 days in both varieties.

Leaf number.

The overall analysis shows that the delays in flowering were accompanied by increases in leaf number, thus indicating that bud initiation was delayed by the treatments. The decrease in leaf number at the lower light intensity during long days reflects the slower rate of growth and increased plastochron during this treatment. Fewer leaves had expanded at the end of the long-day treatment at low light intensity and, since there was no delay in flowering time when plants were transferred to high intensity in short days, the final leaf number to bud was reduced when compared with that of plants at high intensity during the long-day period.

In the previous experiment neither variety showed any increase in leaf number accompanying the delay in flowering at 50°F. during short days. In this experiment, although leaf number was increased by low temperature during short days, the interaction between temperature and light intensity in short days was significant, and from Table VII it can be seen that the increase in leaf number occurred only at reduced light intensity. This interaction between light intensity and temperature may explain the discrepancy between the results of Experiment 2, where a large increase in leaf number accompanied the delay in flowering in Balcombe Perfection and Crensa transferred from 60°F. in long days to 50°F. in short days, and those of Experiment 3 where no such increase occurred.

Flower quality.

Some temperature and light-intensity treatments resulted in failure to flower and only the data for plants at normal light intensity throughout and 60°F. during

TABLE VII.

Effects of night temperature, light intensity and day-length on flowering.

Light intensity		Night temperature °F.		Days to anthesis from start of short-day treatment				Leaf number to bud or at end of the experiment			
				Fred Shoesmith		Balcombe Perfection		Fred Shoesmith		Balcombe Perfection	
In long days	In short days	In long days	In short days	8 hrs.*	14/13 hrs.*	8	14/13	8	14/13	8	14/13
High	High	60(15·5°C.)	60	81	113	82	114	41	41	30	34
		60	50	106	115	116	122	39	41	35	38
		50(10°C.)	60	134+(2)	141+(1)	171+(4)	145	39	43	35	37
		50	50	157+(2)	141	F	148+(2)	42	45	38	31
High	Low	60	60	F	F	141+(1)	167+(1)	65	46	41	41
		60	50	F	182+(3)	187+(3)	179+(3)	75	49	45	42
		50	60	F	188+(1)	175+(2)	179	88	70	46	40
		50	50	F	F	F	F	89	79	62	56
Low	High	60	60	81	113	84	116	32	34	25	30
		60	50	127+(1)	113	151	149	30	34	41	38
		50	60	89	120	154+(2)	153+(2)	33	38	33	33
		50	50	133+(1)	135	176+(3)	153+(1)	32	37	37	33
Low	Low	60	60	F	F	141	167+(1)	39	37	35	40
		60	50	F	F	F	F	48	50	44	43
		50	60	F	F	169+(2)	186+(2)	46	43	43	36
		50	50	F	F	F	F	71	70	57	51

Main effects :

		Mean no. of days to anthesis+	Mean leaf no. to bud, or at end of experiment	
1. Light intensity in long days	High	156·1	47·6	P < ·001
	Low	155·7	40·5	
2. Light intensity in short days	High	129·0	36·0	P < ·001
	Low	183·0	52·4	
3. Temperature in long days	60°F.	145·4	40·8	P < ·001
	50°F.	166·3	47·4	
4. Temperature in short days	60°F.	148·1	41·1	P < ·001
	50°F.	163·8	47·1	
5. Daylength in short days	8-hour	154·5	45·0	N.S.
	14/13-hour	157·4	43·1	

6. Temperature and light intensity in short days ; effect on leaf number

Light intensity	Fred Shoesmith		Balcombe Perfection	
	60°F.	50°F.	60°F.	50°F.
High	37·6	37·8	32·3	36·3
Low	54·4	65·1	40·3	50·3

Significant difference = 3·66

* Day-length during short days.

\+ Where plants failed to flower the number of days to anthesis was taken as 190, i.e. the number from the commencement of short days to the end of the experiment ; the number of plants which failed to flower is given in brackets.

F, All plants failed to reach anthesis.

PLATE I.

Fig. 1.

Effect of low temperature during long or short days on development of the terminal inflorescence of chrysanthemum.

Left, low night temperature (50°F.) during short days and *right*, during long days. *Top*, "Balcombe Perfection"; *bottom*, "Fred Shoesmith".

[*face p. 170*

TABLE VIII.

Effect of night temperature and day-length during short days on flower diameter.

Day-length	Mean flower diameter (cm.)			
	Fred Shoesmith		Balcombe Perfection	
	60°F. (15·5°C.)	50°F. (10°C.)	60°F.	50°F.
8 hours	8·6	10·6	8·1	11·5
14/13 hours	9·3	11·7	9·2	12·2
Significant difference at P=0·05	1·24			

1. Effect of day-length: 8 hours 9·7, 14/13 hours 10·6 } P = ·01
2. Effect of temperature: 60°F. 8·8, 50°F. 11·5 } P < ·001

long days have been given (Table VIII). Both night temperature and day-length affected flower diameter ; no interaction occurred, the treatment effects being almost completely additive. Temperature had the greatest effect and flower diameter was increased by 2-3 cm. in plants transferred to 50°F. during short days. A smaller but highly significant effect of day-length occurred and flower size was increased by up to 1 cm. in the longer day-length. These results lend support to the suggestion that one of the factors leading to poor flower quality during the winter months is the very short day-length occurring at that time. Post and Lacey (1951) have recommended interrupting the short-day treatment with intercalated long days to improve flower quality in standard chrysanthemums ; this interrupted short-day treatment, however, delays flowering as did the long-day-length treatment used here. Moreover, the effect of short day-lengths on flowering quality is probably very small compared with the effect of low winter-light intensity.

Ray-floret counts were made on Balcombe Perfection only since ray florets in the centres of the Fred Shoesmith flowers were found to be withered. At high light intensity, differences between treatments were small and the increased size of flowers must, as before, have resulted from increased growth in length of the individual ray florets. At reduced light intensity, the decrease in flower diameter was found to be accompanied by a smaller number of ray florets.

DISCUSSION.

Time of flowering.

(a) *Temperature.* When compared with a continuous temperature of 60°F. a night temperature of 50°F. or below delayed flowering in several English " standard " glasshouse chrysanthemums. The amount of delay depended on the variety, on the stage of growth when the low temperature was given, and on the light intensity.

During short-day induction a low night temperature markedly delayed flowering in several varieties ; these would be classified in the " thermo-positive " group of

Cathey (1954a). Once the bud became visible, however, a lower night temperature no longer delayed flowering. The optimum temperature appeared to be about 50°F., since plants at 40°F. night temperature were delayed by a few days. In these experiments no attempt was made to determine how many short days at 60°F. are required before transfer to 50°F. fails to delay flowering. Samman (1958) has reported that no appreciable delay due to low temperature occurs after ten short days at 60°F. Some unpublished results from this laboratory, however, suggest that varieties differ in their behaviour ; whereas flowering in Mayford Crimson was not delayed on transference to 50°F. night temperature after 10-15 short days at 60°F., few plants of Finale flowered when transferred to 50°F. even after 30 short-days at 60°F.

The effect of low night temperature during short-day induction may be regarded as a photoperiodic effect. The inductive dark reaction has been shown to be dependent on temperature and in some short-day plants a low temperature may reduce or annul its effect (Leopold, 1951 ; Lang, 1952 ; Liverman, 1955). In most of the varieties used, the effect of the low night temperature during short-day induction was to delay flowering, with little or no increase in leaf number, and the characteristic effect of low temperature appeared to be a suppression or delay in floret initiation and development rather than any effect on capitulum initiation. In many varieties the initiation of the inflorescence bracts and capitulum (break bud formation) occurs in long days, with little or no delay when compared with short days (Mason, 1957) ; in all glasshouse chrysanthemums the initiation and development of florets, however, require short days. It is this latter stage, therefore, which is suppressed or delayed when low night temperatures are given during short-day induction. A notable exception occurred in the variety Mayford Crimson, where plants transferred to low temperature remained vegetative for a long period and large increases in leaf number occurred. In this variety capitulum initiation is delayed in long photoperiods, with a large increase in leaf number (Mason, 1957), and its behaviour in short days at low temperature is consistent with this.

A low night temperature during the $5\frac{1}{2}$ to $6\frac{1}{2}$ week long-day period caused considerable delays in flowering, even though plants were transferred to 60°F. during short-day induction. Moreover this delay was accompanied in most varieties by increases in leaf number, thereby indicating that both capitulum and floret initiation were delayed. A further characteristic of this treatment was that the terminal inflorescence bud often failed to develop to anthesis ; since only the terminal bud was recorded, these plants were considered to have failed to flower. In fact, however, on transfer to 60°F. in short days, the lateral shoots formed buds which developed to anthesis and many of these plants flowered before plants at 50°F. in short days, where the terminal inflorescence bud developed slowly to anthesis. Although at present it is difficult to suggest any reason for this type of behaviour, it is clear that a period of low temperature (50°F. or below) at any stage until the bud becomes visible may delay flowering.

(b) *Light intensity*. The delaying effect of low light intensity during the short-day period has been recorded before for the American variety Goldcoast by Watson and Andrews (1953) and for the variety Sunbeam by Schwabe (1956) ; Watson and Andrews have also noted the interaction between temperature and light intensity. The major new point arising here is that only the light intensity during short-day induction affected the time of flowering. The effect of low light intensity appears,

therefore, to be directly photoperiodic, as in some other short-day species for which a period of high light intensity during the day has been found to be essential for the subsequent dark period to be effective. The general carbohydrate status of the plant apparently has little effect, since plants previously at low intensity flowered with no delay provided that normal light intensity was given during short-day induction, whereas induction failed in plants of high carbohydrate status if they were transferred to low intensities during the induction period. It would be of interest to determine whether the period of high light intensity for chrysanthemum could be replaced by sugar feeding, as recorded for *Xanthium pennsylvanicum* by Liverman and Bonner (1953).

An interaction between low light intensity and low night temperature was found and, whereas at normal light intensity leaf number to bud was not increased in either Fred Shoesmith or Balcombe Perfection, there was a marked low-temperature delay in terms of leaf number at the reduced light intensity.

(c) *Day-length.* In the final experiment two day-lengths were included, primarily to investigate the effect of this environmental factor on flower quality ; however, when the other environmental factors were favourable for flowering, the longer day-length delayed flowering by about 30 days. This day-length consisted of 14 hours for one week, followed by 13 hours. Post (1947) originally reported that a day-length of less than 14½ hours was necessary for capitulum initiation, and less than 13½ hours for floret initiation. The present results show however that, in the two late flowering varieties used, a day-length considerably shorter than these threshold levels markedly hastened flowering. Cathey (1957) has recently shown that the later the natural flowering date of a variety the shorter is the threshold day-length for flowering in American spray varieties.

Flower quality.

Flower quality was shown in these experiments to be affected by night temperature, light intensity and day-length. Light intensity had the greatest effect, the few flowers which opened under the reduced light intensity being small and containing few ray florets. Temperature also had consistently a large effect and a lower night temperature increased flower size and quality as compared with 60°F. throughout ; the temperature after the bud became visible primarily determined flower size. The optimum appeared to be about 50°F. ; a temperature of 40°F. produced large blooms, but these were flatter and of a somewhat inferior market quality. A longer day-length during short-day induction resulted in a small but significant increase in flower diameter. The effect of day-length was only tested during the autumn months when the natural light intensity was poor ; its effect during high summer is not known. The temperature factor was, however, tested during both summer and winter and found to have a consistently large effect on all varieties grown. The increased flower diameter in both low temperatures and long days was found to result primarily from an increase in length of individual florets rather than from an increase in their number ; both low temperature and longer days must, therefore, increase the amount of corolla growth in ray florets. The failure to expand the centre florets at 60°F., which was observed in American Beauty, and the failure to reflex in reflexed varieties may, therefore, be simply a result of reduced growth in length of the ray-floret petals.

From the experiments described it is clear that the chrysanthemum has a

rather precise temperature requirement for most rapid flowering coupled with maximum flower quality, and that this may vary with variety. Flowering may also be modified by photoperiod and light intensity. While precise temperature requirements could be determined for each variety, 60°F. until the bud becomes visible, followed by a lower night temperature of 50-55°F., would still appear to be the most generally suitable practical recommendation for most varieties.

SUMMARY.

A low night temperature of 40-50°F. (4·5-10°C.) has been found to delay flowering in several varieties of English glasshouse chrysanthemums when compared with 60°F. (15°C.) throughout.

When low night temperatures were given during long days, the delay in flowering was usually accompanied by an increase in leaf number to bud formation. The terminal inflorescence bud frequently failed to develop to anthesis when plants were transferred from low temperatures during long days to 60°F. during short days.

When low night temperatures were given during short-day induction, the delay in flowering was not usually accompanied by an increase in leaf number to bud formation ; an exception was the variety Mayford Crimson.

When low night temperatures were given after the bud had become visible macroscopically, little or no delay in flowering occurred.

A reduced light intensity during short days markedly delayed flowering : an interaction between light intensity and temperature occurred and, at low light intensity, the leaf number to bud formation was increased by low night temperatures during short-day induction. Light intensity during long days did not affect the time of flowering.

Flower diameter was increased by low night temperature and was primarily determined by the temperature after the buds became visible macroscopically. With favourable light intensity and temperature, flower diameter was greater when short-day induction consisted of 14-hour followed by 13-hour photoperiods than when 8-hour photoperiods were given ; the former day-length treatment, however, delayed flowering.

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THE SPACING OF WEST AFRICAN AMELONADO COCOA IN GHANA

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ALTHOUGH Ghana exports more cocoa than any other country the production is almost entirely from small peasant farms. Typically these farms comprise a few acres of secondary rain forest partly cleared of ground vegetation and planted at random with cocoa at a high density. As the cocoa matures, natural thinning occurs. This, combined with regeneration by rodent-sown seeds, with a natural "coppicing" due to old trees breaking and basal chupons developing, and with damage by capsids and other pests, produces a population of cocoa trees of all ages. This population, growing together with other species, forms a community similar to any naturally occurring plant community, in that the cocoa adjusts itself in relation to the soil, shade, competition and climatic elements of its environment.

In Ghana, planting of cocoa in new regions and the replanting of areas cut-out because of swollen shoot virus call for a more scientific approach. An experiment, which is the subject of this paper, was thus designed to investigate the optimum spacing at which West African Amelonado cocoa should be grown and the influence of the various spacings on establishment and yield.

There are many different opinions concerning the spacing of cocoa. It is grown at relatively close spacings in Ghana, 6 or 7 ft. apart. Van Hall (11) states that in Surinam and tropical South America cocoa is commonly grown at 15-24 ft. apart. Little experimental work has been done on this subject. Freeman (5) describes a series of plantings at River Estate, Trinidad, in which four plots planted at 12, 14, 16 and 18 ft. spacings were recorded. The 12 ft. spacing produced the highest yields up to the 6th year, but was then out-yielded by the 14 ft. spacing. Russell (7) followed by Kowal (6) reports a spacing trial in Nigeria. Russell concluded that, over a range of 800 to 1,100 trees to the acre, yield per acre was little affected by spacing, but that at wider spacings the yield declined. Kowal further pointed out that the average weight of wet beans and the number of pods per tree increased with decreasing stand density, but not sufficiently to increase the yield per acre at lower densities. This trial is, however, yielding well below its potential and is obviously growing in suboptimal conditions (Cunningham, 3).

Van der Knapp (10) in Indonesia reports higher yields, in the first three years of cropping, from cocoa growing at 4×2, than at 4×5 or 4×8 metres.

THE SPACING TRIAL.

Lay-out.

The site chosen was $8\frac{1}{2}$ acres of secondary rain forest. The area had been partly farmed before and a certain amount of cocoa was present under a dense overhead shade of numerous tree species. The soil is a good cocoa soil, of the

W.A.C.R.I. and Koforidua soil series of Charter (2). It is a free-draining, rich, sandy loam, developed over a hornblende granodiorite substrate. The soil is a deep one, becoming clayey in nature at some 12 inches below the surface (Brammer, 1).

The experiment consists of eight different spacings, randomized in seven blocks. The treatments chosen were intended to cover the range of densities commonly met with in random-planted farmer's cocoa. Each treatment plot is 60 ft. square. The choice of spacings was therefore limited, in order to fit a convenient number of trees into each plot. Each plot is surrounded by one guard row at the same spacing as the treatment. Details of the treatments are given in Table I.

Table I.

Data of the spacing treatments.

Spacing (ft. × ft.)	Trees/plot	Trees/acre
15 × 15	16	192
12 × 12	25	302
10 × 10	36	436
7·5 × 7·5	64	774
6 × 7·5	80	968
6 × 6	100	1,210
5 × 5	144	1,742
4 × 4	225	2,722

Establishment.

The undergrowth was cleared to facilitate lining and pegging prior to planting. The plots were laid down with a 20 ft. wide space between them and bananas planted for shade at 10 ft. apart in the centre of these surrounds. All forest trees were then removed and any cocoa present was cut out below ground level. Temporary shade of tree cassava (*Manihot* sp.) was planted in the endeavour to provide equal shade on all treatments. The ground cover was left to protect the soil against leaching and insolation. Additional permanent shade of *Erythrina senegalensis* was planted at 40 ft. intervals.

When the shade growth was considered satisfactory, cocoa was planted as seed at stake. Three seeds were planted at each stake and the seedlings singled at the end of the second dry season. Establishment under these conditions was satisfactory. No records were taken of germination or survival of the young seedlings. Establishment was begun in April 1947 and completed before the dry season in August of that year.

Maintenance.

The general maintenance of the trial consisted of regular "brushing" of the weed growth and control of the shade. By the sixth year after planting, which was the first year of bearing, the shade consisted of forest trees which had been allowed to regenerate and the planted *E. senegalensis*. The tree cassava and bananas had been removed. The result was approximately a 60% shade over the cocoa. The *E. senegalensis* proved unsatisfactory as a shade tree, the crown being too small when grown under these conditions. Between the sixth and eleventh years, this

shade was considerably reduced by poisoning, until at the present time there is only 15-20% overhead shade,

Performance of the cocoa.

By the sixth year, the cocoa had formed a complete canopy over the soil at densities exceeding the 10×10 ft. spacing. At the eleventh year, only the 15×15 ft. spacing had not closed its canopy. Where a complete canopy had formed, a natural weed control due to lack of light made maintenance easy. A deep leaf litter covered the soil, providing a natural mulch. Invasion by weeds and the presence of little leaf litter were features of the wide spacings.

There are considerable differences in the growth habit of the cocoa at different spacings. A gradient can be seen from 4×4 ft., with tall trees of thin girth and limited development of the fan branches, to 15×15 ft., with shorter trees of wide girth and greater development of the laterals. These differences are well illustrated by Tables II and III which show girth measurements and the ratio of pods produced on trunk and branches. The records were taken from 16 individually recorded trees in each plot. At the closer spacings many of the trees have suffered from competition within the cocoa, being very thin, poor trees which have never borne any crop.

Results.

The statistical analysis of the records from an experiment such as this, where the number of trees per plot varies from 16 to 225 and the individual tree-to-tree variation is very high, presents some difficulty, so that the significance of smaller differences in yield or size of tree is very dubious. Nevertheless, the larger differences and the trends, as illustrated in Fig. 1, are so evident that statistical analysis is hardly necessary to prove them. Where the yields are compared on an acreage basis, as in Table V, the differences can be compared statistically with more confidence and " significant differences " are only shown in this Table.

Girth measurements were recorded at a height of six inches above the ground on 16 trees in each plot. As may be seen in Table II the differences in 1955 were slight. By 1958 the trees had grown further, and competition had restricted growth at the close spacings. At the wider spacings such competition had been much smaller.

Table II.

Mean girth per tree.

Spacing (ft. × ft.)	Mean girth	
	1955	1958
15×15	9·9	17·77
12×12	10·0	17·06
10×10	10·1	16·34
7·5×7·5	10·3	14·87
6×7·5	9·5	14·97
6×6	9·4	13·03
5×5	9·4	12·18
4×4	7·5	9·89

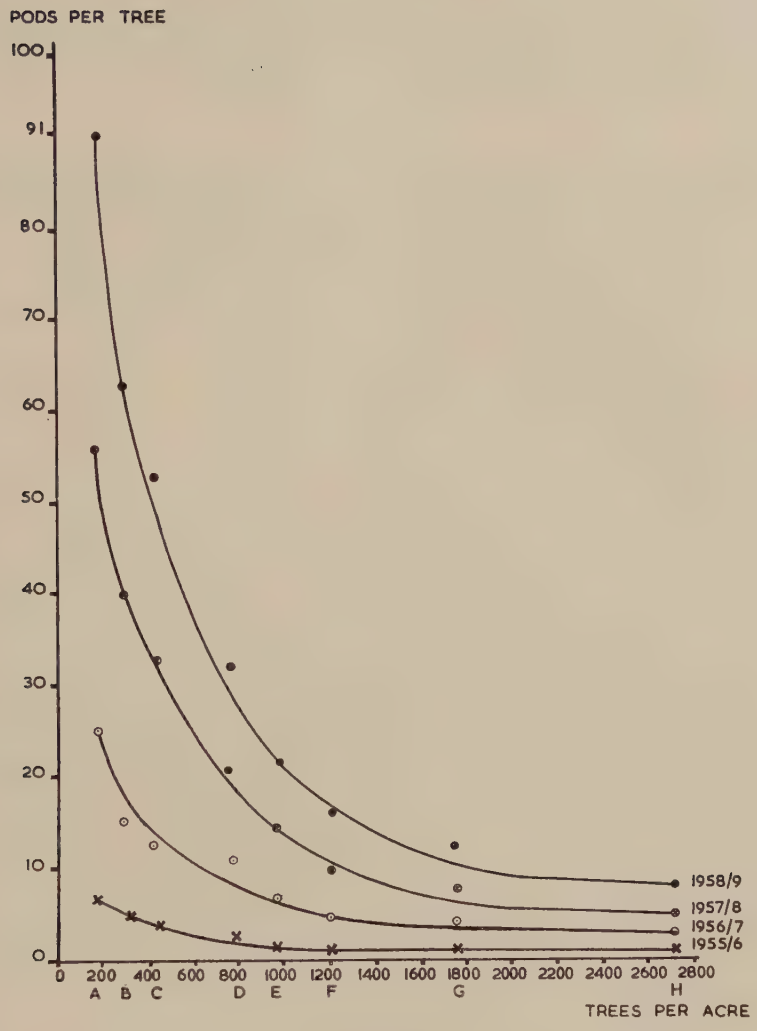

Fig. 1.

Relation between number of trees per acre and number of pods per tree, over a period of four years. Spacing (ft. × ft.): A, 15 × 15; B, 12 × 12; C, 10 × 10; D, 7·5 × 7·5; E, 6 × 7·5; F, 6 × 6; G, 5 × 5; H, 4 × 4.

Table III illustrates the increasing importance of the branch-crop, especially at the wider spacings, as the trees reach maturity. The branch-crop forms more of the total crop at wide than at close spacings. These two Tables when considered together illustrate the difference in habit between the trees at different spacings. At the wide spacings, the development of the trees is still poorer than expected by comparison with other plots of cocoa. This is probably due to the fact that the shade

was too heavy in the early years. Heavy shade has a detrimental effect on the early growth of the cocoa, similar to the effect of close spacing. To judge from other plots, much better trees, with better branch development, would have resulted if the shade had not been so heavy in the earlier years.

TABLE III.

Percentage of total pods produced on the trunk under the different treatments over 4 years.

Spacing (ft. × ft.)	% pods produced on trunk			
	8th year	9th year	10th year	11th year
15×15	77·2	56·1	39·7	29·5
12×12	71·8	62·5	41·5	31·6
10×10	75·5	79·4	48·0	37·6
7·5×7·5	77·5	75·0	56·2	46·1
6×7·5	83·0	76·7	64·7	58·5
6×6	74·3	76·9	70·8	58·7
5×5	89·5	77·7	69·0	61·4
4×4	81·0	77·8	73·1	58·9

Yield.

From the first year of bearing to the present time yield has been recorded as the total number of pods produced. This was split into good pods and discarded pods, the latter being such as do not contain fermentable cocoa beans because of severe black pod disease, rodent damage and other subsidiary causes. The figures given, however, represent total crop produced by the tree. It is felt that, although black pod disease may be affected by spacing (Thorold, 9), the main effect of the spacings on yield is represented by the figures given. The level of disease and damage is generally very low, as a result of a regular harvesting programme at two-weekly intervals and regular spraying against capsids. Until the sixth year the few pods produced were more or less in proportion to the number of trees present. The closer spacings therefore showed a better yield on a per-acre basis. The first year of appreciable bearing, however, was the sixth. The results shown in Tables IV and V show the number of pods per tree and the number of pounds of dry cocoa

TABLE IV.

Number of pods per tree at the different spacings over 5 years.

Spacing (ft. × ft.)	Number of pods per tree					Total
	7th year	8th year	9th year	10th year	11th year	
15×15	4	7	25	55	91	182
12×12	3	5	16	40	62	126
10×10	2	4	13	33	53	105
7·5×7·5	1	3	12	21	32	69
6×7·5	1	2	7	15	22	49
6×6	1	2	6	10	16	35
5×5	1	1	5	8	13	28
4×4	1	1	2	5	8	17

produced per acre. The latter figure is calculated on a basis of twelve pods producing one pound of dry cocoa, a figure which is fairly constant with West African Amelonado cocoa at W.A.C.R.I.

Table V.

Pounds of dry cocoa per acre produced at different spacings over 6 years.

Spacing (ft. × ft.)	Pounds dry cocoa per acre						Total
	6th year	7th year	8th year	9th year	10th year	11th year	
15×15	7	63	109	404	889	1,466	2,938
12×12	9	73	129	397	1,003	1,570	3,181
10×10	11	89	141	479	1,213	1,925	3,858
7·5×7·5	10	96	190	748	1,376	2,082	4,502
6×7·5	8	53	146	603	1,201	1,788	3,799
6×6	5	75	155	562	1,016	1,650	3,463
5×5	8	96	182	694	1,188	1,903	4,071
4×4	6	50	111	551	1,034	1,833	3,585

For totals : sig. diff. at P=0·01 is 145, at P=0·02 is 129.
For 11th year : sig. diff. at P=0·01 is 437, at P=0·02 is 391.

The most striking effect of the spacing is that on the number of pods per tree (Table IV). It can be seen that more pods are produced per tree as the spacing increases. This result was not clearly demonstrated by Russell (7) in Nigeria but was reported by Kowal (6). This agrees well with the vigour of the trees as measured by girths in Table II. The girth in 1958 is correlated with the yield per tree (Correlation co-efficient, +0·906). Fig. 1 shows graphically the pattern of the number of pods per tree over the six years in question.

Economically, the important figure is the amount of cocoa produced per acre. It may be asked whether it is better to have a large number of trees each producing few pods, or fewer trees producing more pods each. Squibbs (8) states that : " There is reason to believe that there is no best planting distance for amelonado cocoa, even in one locality or on one soil type. Random close planting and allowing the trees to thin themselves is probably the best practice." This theory is understandable when the similarity of the graph (Fig. 1) to a hyperbola is noted. If a hyperbola had been produced, reduction in tree population would be compensated for by a corresponding increase in pods per tree. However, under the present conditions, a perfect hyperbola is not produced, because the peaks at $7\frac{1}{2}\times7\frac{1}{2}$ ft. and 5×5 ft. in Fig. 2 are highly significant. These peaks occur under the edaphic, shading, varietal and climatic conditions under which the trees have grown. Other environmental conditions might well have produced a hyperbola.

Table V shows extremely high yields per acre in the later years. The increase over the years is due partly to an increasing maturity of the trees and partly to a decrease in the shade. On a similar soil and under similar conditions it has been shown that high yields are brought about by shade removal (Cunningham and Lamb, 4).

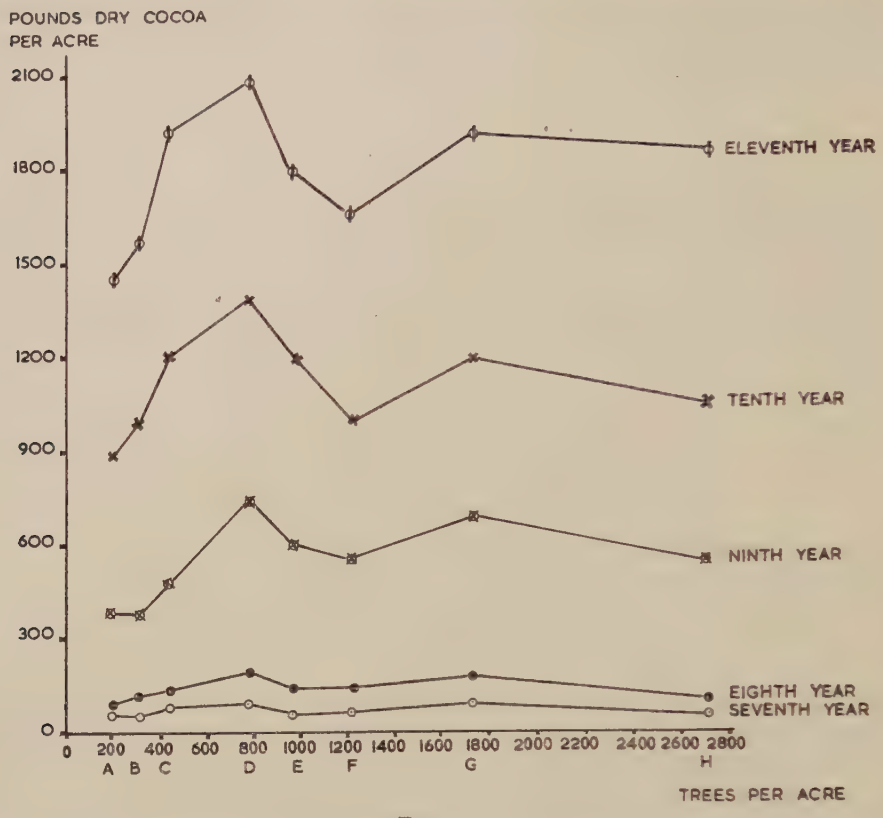

FIG. 2.

Relation between number of trees and yield of dry cocoa per acre, over a period of five years. Spacing as in Fig. 1.

CONCLUSIONS.

It is clear that, under the conditions of the experiment, a reduction in tree population brings about a corresponding increase in the number of pods per tree. The relationship between tree density and pods per tree is hyperbolic in nature, but deviations from the hyperbola under the conditions of the experiment have proved significant. Thus Fig. 2 shows a double peak in the graph, one at $7\frac{1}{2} \times 7\frac{1}{2}$ ft. and the other at 5×5 ft. Competition effects probably determine the exact shape of the curve. At densities greater than about 1,800 trees per acre, high competition between the trees results in many of them being suppressed and not contributing to the canopy. These trees do not bear fruit and there are only a few pods on the remainder. Between 1,200 and about 700 trees per acre, such competition is greatly reduced. Probably root room becomes optimal and competition for nutrients thus reduced. This, combined with more space and light for maximum development of the lateral branches, probably causes a rapid increase in pods per tree which, in spite of a reduction in tree population, results in an increase in yield per acre. At

tree densities less than about 700, in spite of a continuing increase in the performance of each tree, the yield per acre drops because tree population becomes the limiting factor. At such wide spacings maximum use is not being made of the air space. The canopy is not closed, thereby permitting weed growth and its subsequent competition, and the roots are not fully exploiting the available soil volume.

Further investigations of root and canopy development under different spacings are required before these competition factors can be fully elucidated.

We may therefore conclude that it is uneconomical to grow cocoa at less than 680 trees to the acre, at least for the first 11 years. This spacing (8×8 ft.) is a convenient one for maintenance, spraying and harvesting. At closer spacings, in addition to a possible reduction in yield, agronomic operations become difficult and expensive.

SUMMARY.

A spacing trial at W.A.C.R.I. is discussed in relation to yield, habit and general performance of the trees. It was concluded that, under the conditions of the experiment, a spacing of $7\frac{1}{2} \times 7\frac{1}{2}$ ft. was optimum for high yields and that, therefore, Amelonado cocoa in Ghana should be grown at approximately this spacing.

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A LONG-TERM MANURIAL EXPERIMENT WITH HOPS

THE EFFECT OF HEAVY MANURING ON SOIL FERTILITY AND ON THE YIELD, LEAF MINERAL CONTENT AND RESIN CONTENT OF THE VARIETY FUGGLE

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In England the commercial manuring of hops was formerly very haphazard and usually excessive. The fact that the crop is an expensive one to grow, and that expenditure on fertilizers forms a relatively small item in the total cost of production, led to the practice of applying heavy dressings of both organic and inorganic fertilizers, often purely as a safety measure on the assumption that, even if no benefit accrued, no harm would be done.

There has been little experimental work on hop manuring in this country and, apart from a small trial comparing Peruvian guano with a complete inorganic manure (Dent *et. al.*, 1938), the only hop manurial experiment of modern design previously reported is that carried out by Burgess (1950) in the period 1930-1948. This experiment was, however, limited to testing different times and rates of application of nitrogen fertilizers.

In consequence, it was decided in 1949 to lay down a more comprehensive NPK trial, comparing a very high level of manuring, on the lines still commonly adopted by commercial growers at that time, with a lower level " standard " manurial scheme as recommended by Burgess (1949). Through the courtesy of Guinness Hop Farms Ltd., the trial was established on their farm at Bodiam, Sussex, on land which had not previously carried hops ; the garden was planted with cuttings of the Fuggle variety in Spring 1949, spaced at 7×7 feet square.

Soil and experimental design.

The soil is a very fine sandy loam of the Pembury series, derived from the Tunbridge Wells Sand, a soil commonly found in the hop-growing areas of the High Weald in Kent and East Sussex. It was of low fertility ; prior to the experiment, chemical analysis gave very low values for available phosphorus, potassium and magnesium.

The experiment consisted of 32 plots in four blocks of eight treatments—N, P, K and Mg each at two levels, the NPK interaction being confounded with blocks. The whole of these 32 plots received a basal dressing of 14 tons dung per acre annually plus inorganic fertilizers. In addition, a subsidiary trial was planned on a strip of land running through the centre of the experimental area, to give a broad comparison between " dung and inorganics " and " inorganics only " treatments. Each dunged

plot consisted of 12 plants with single guard rows between each plot. Double guard rows were left between the dunged plots and the inorganic strip, which was divided into four 18-hill plots separated by single guard rows.

For simplicity in presentation, the experimental data and results for the dunged plots are given first.

DUNGED PLOTS.

Materials and methods.

Manurial treatments—1949 to 1953.

For the first two years of the trial only the phosphate and potash treatments were applied as detailed below ; the whole of the dunged area received a uniform dressing to supply 300 lb. N per acre.

In 1951 the full range of proposed treatments was introduced ; the " standard " treatment supplied, per acre, 300 lb. N, 200 lb. P_2O_5 and 200 lb. K_2O. These will be referred to as treatments $N_1P_1K_1$. The " high level " dressings applied were, per acre, 400 lb. N, 500 lb. P_2O_5 and 400 lb. K_2O ($N_2P_2K_2$). These quantities of nutrients were supplied partly as dung and partly as inorganic fertilizers, the allowance made for the N, P and K in the dung being based on the analysis of samples taken from the dung used in each year. A further treatment tested was presence and absence of magnesium—treatments Mg_1 (55 lb. Mg per acre) and Mg_0 (no Mg). The inorganic fertilizers used were " nitro-chalk ", superphosphate, muriate of potash and Epsom salts.

Manurial treatments—1954 to 1958.

In 1954 the treatments were changed, primarily because it was considered desirable to revise the phosphate treatments, but also because of doubts at the time as to the value of basing accurately calculated applications of nutrients on the analysis of such a variable material as dung. In consequence, it was decided to give annual applications of fixed quantities of N, P and K fertilizers irrespective of the analysis of the dung applied.

The nitrogen treatments were maintained at slightly lower levels than in previous years, to make some allowance for the nitrogen in the dung.

The alterations in the phosphate treatments were more drastic. The available phosphorus in the soil on the P_2 plots had been raised, by 1953, to a level approaching " very high " and it was considered desirable to measure the yield of hops on these plots without further additions of superphosphate, and to compare this with the performance of hops receiving a heavy annual dressing of superphosphate on the P_1 plots, which showed a much lower available phosphorus status.

The response to the high level potash treatment (K_2) had become very small by 1953 and soil analysis results suggested that the rate of increase of available potassium from this treatment was slow, possibly as a result of potash fixation. In an attempt to speed up the rate, the dressings on both the K_1 and K_2 plots were increased considerably.

The magnesium treatments remained unaltered.

The revised treatments supplied the following quantities of nutrients per acre, in addition to the nutrients in the dung :

" Standard " treatment ($N_1P_1K_1Mg_0$)—140 lb. N, 200 lb. P_2O_5, 200 lb. K_2O, nil Mg.

" High level " treatment ($N_2P_2K_2Mg_1$)—260 lb. N, nil P_2O_5, 400 lb. K_2O, 55 lb. Mg.

Soil analysis.

Soil samples to two depths (0-6 in. and 6-12 in.) were taken from all plots each year in mid-winter. These were analysed for available P, K and Mg, using an extract prepared by shaking, for two minutes, one part of air-dry soil to two parts of Morgan's (1937) reagent. Soil pH was also measured. In addition, from 1954 onwards determinations were made of organic carbon by the method of Walkley and Black as described by Piper (1942). In the three years 1954-1956, exchangeable K and Mg were also determined by leaching with neutral normal ammonium acetate (Peech, 1945), as a check on the " available " nutrient determinations ; satisfactory correlations were found.

Leaf samples.

Leaf samples were taken annually. To obtain comparable samples, fully expanded but not senescent leaves were taken at the end of June or beginning of July, when the plant had made its main flush of extension growth, and before the development of cones. After removal of the petioles, the laminae were dried at 100°C. and analysed for total N, P, K, Mg and Ca.

Resin analyses.

Samples of cones for determination of total soft resins were taken in each year from 1951 onwards. Estimations of the alpha acids and beta fraction were also made in some years. The method of analysis used was that of Ford and Tait (1932).

Results.

Yield.

The plots were harvested in each of the years 1950-1955 and again in 1958. Though there was some evidence of antagonism between high potash and magnesium, interaction effects between treatments were, in general, inconsistent and non-significant, and consequently only the results for the main treatment effects are presented (Table I).

Table I.

Effect of manurial treatments on the yield of dry hops, in cwt. per acre.

Year	Treatment means								Yearly mean
	N_1	N_2	P_1	P_2	K_1	K_2	Mg_0	Mg_1	
1950*	—	—	10·1	13·0	11·0	12·0	—	—	11·6
1951	28·4	27·2	26·4	29·2	26·8	28·7	27·7	27·9	27·8
1952	14·0	13·1	13·0	14·2	13·0	14·2	13·1	14·1	13·6
1953	13·2	13·2	12·7	13·7	13·1	13·3	13·5	12·9	13·2
1954	8·6	9·4	8·8	9·2	8·9	9·1	8·8	9·2	9·0
1955	22·8	19·2	20·3	21·7	20·8	21·2	20·7	21·3	21·0
1958	14·5	15·3	15·1	14·8	15·5	14·3	14·7	15·1	14·9

* Differential nitrogen and magnesium treatments not applied in this year.

In 1950, although the plants were still young by commercial standards, they produced a good crop of hops. In the succeeding years the crop showed marked

seasonal variations, though in 1954 the very low yield obtained could be attributed in part to a severe late attack of Downy Mildew.

When the effects of differential manuring are considered, it can be seen from Table I that the response to nitrogen was inconsistent, though it is noteworthy that in the years of high average yield (1951 and 1955) high nitrogen depressed yield appreciably, the effect being significant ($P<0{\cdot}01$) in 1955. The yield responses to the other manurial treatments showed certain interesting correlations with changes in the available nutrients in the soil, and are discussed below in conjunction with the soil analysis data.

Soil analyses—available nutrients.

Mean data for the 0-6 in. samples are shown in Figs. 1, 2 and 3, in which the histograms represent the yield response to the different manurial treatments tested, expressed as a percentage of the mean yield in order to eliminate yearly variations in crop. Changes in the level of available nutrients in the 6-12 in. samples largely paralleled those found for the 0-6 in. samples and are not reported in this paper.

Available phosphorus. Fig. 1 (a) shows the changes in available phosphorus at the two levels of phosphatic manuring applied annually in the period 1948-1953. Initially the soil contained only a trace of available phosphorus and at the end of the first year the build-up was slight and the difference between the P_1 and P_2 treatments was small and non-significant. Later, however, there was a rapid increase in available phosphorus, which initially was more pronounced at the P_2 level, the difference established between the P_1 and P_2 levels being significant ($P<0{\cdot}01$) throughout this period. At first there was a large yield response to the high phosphate treatment, which was significant in 1950 ($P<0{\cdot}01$) and in 1951 ($P<0{\cdot}05$), but the response then decreased as the level of available phosphorus rose and it was non-significant in 1952 and 1953.

The changes in available phosphorus in the second period of the trial, from 1954 to 1958, are shown in Fig. 1 (b). In this period the available phosphorus on the P_2 plots continued to rise, although no inorganic phosphate was applied to the plots, the increase being due, presumably, to the phosphate in the annual dressings of dung. On the P_1 plots, now receiving 200 lb. per acre P_2O_5 as superphosphate, in addition to dung, the rise in available phosphorus was more rapid, as would be expected, and by 1957 the level was above that on the P_2 plots. In this period, for the first two years, the yield on the P_2 plots continued to be higher than on the P_1 plots, though the difference was non-significant. By 1958, however, when the levels of available phosphorus on both series of plots were comparable, yields with both treatments were similar though slightly higher with the P_1 treatment.

Available potassium. Fig. 2 (a) shows the build-up of available potassium at the two levels of potash manuring applied annually in the period 1948-1953. Initially the soil contained a very low level of available potassium, but by the end of the first year the level rose appreciably, particularly with the K_2 treatment, the difference between the plots being significant ($P<0{\cdot}01$). Available potassium continued to rise slowly over the next two years, and the difference between the treatments, though continuing to be significant, did not increase. From 1951 to 1952 there was a more rapid increase at the K_2 level, but in 1953 the results showed a fall in available potassium with both treatments, possibly due to the dry season. On the K_1 plots, which received on average 1 cwt. per acre muriate of potash annually in addition

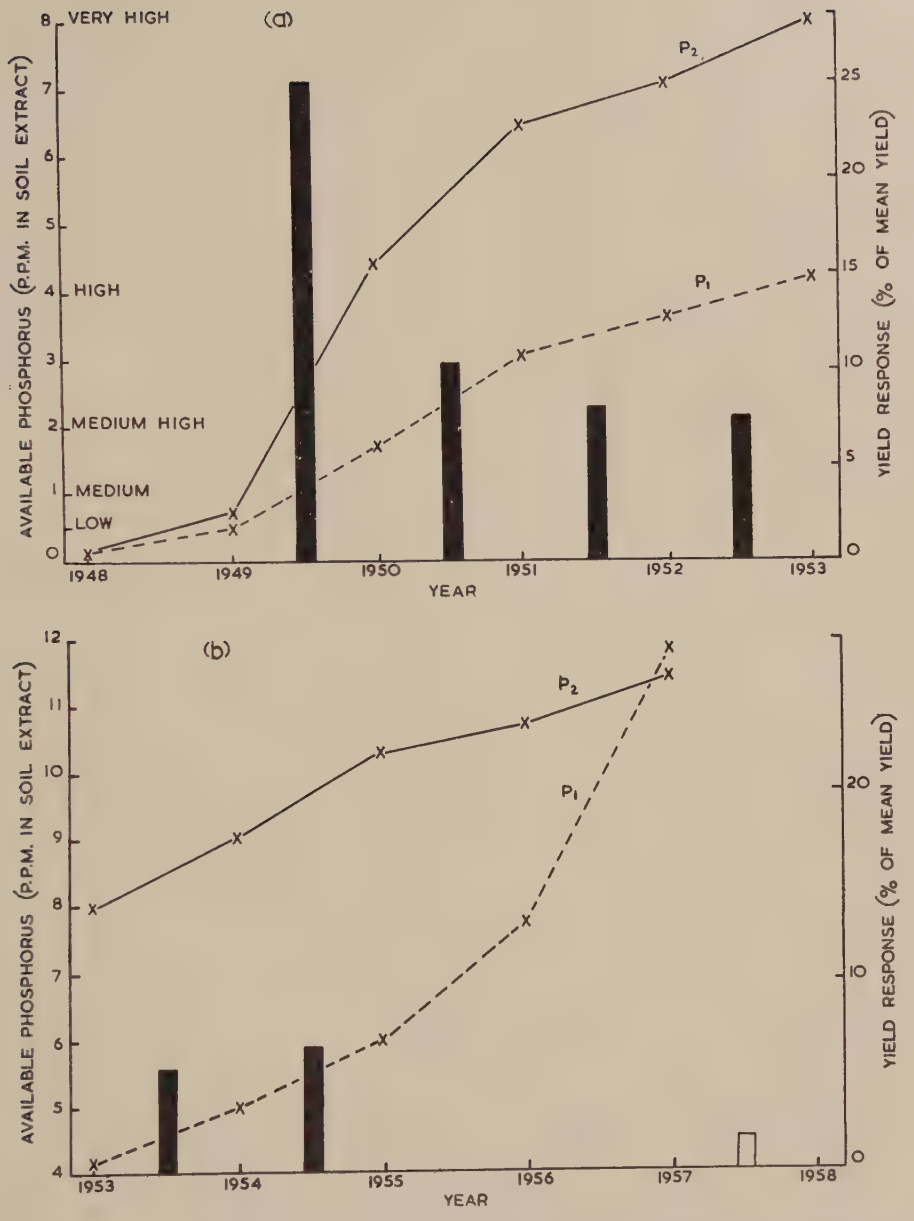

FIG. 1.

Annual increase in soil-available phosphorus (sampled mid-winter, 0-6 in. depth) at two levels of phosphate manuring, and the associated yield response of hops harvested in the following summer.

(a) Period 1948-1953 : P_1, 200 lb. per acre total P_2O_5 x — — — — — x
P_2, 500 lb. per acre total P_2O_5 x————————x
Yield response to P_2 treatment ■+ve

(b) Period 1953-1958 : P_1, 14 tons dung + 10 cwt. superphosphate per acre x — — — — — x
P_2, 14 tons dung per acre x————————x
Yield response to P_2 treatment ■+ve, □—ve.

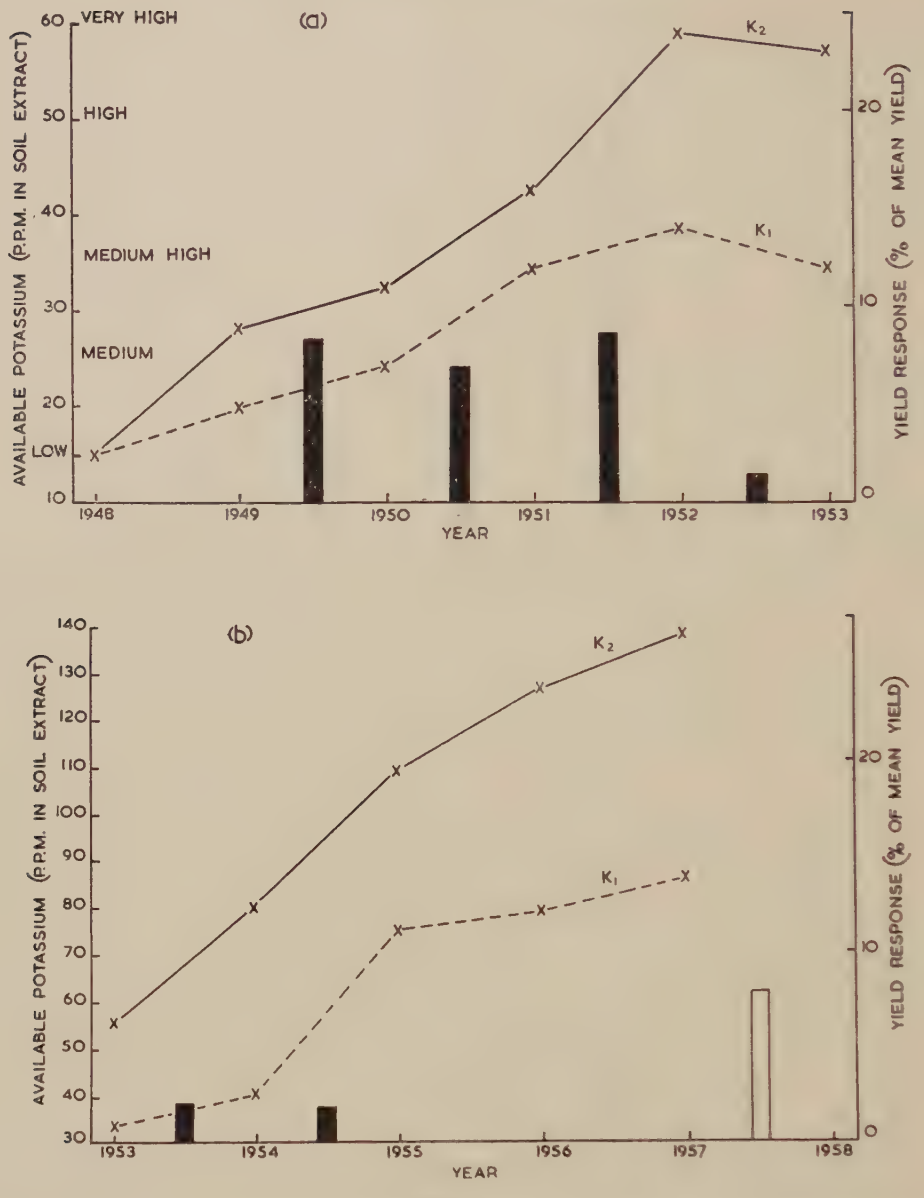

FIG. 2.

Annual increase in soil-available potassium (sampled mid-winter, 0-6 in. depth) at two levels of potash manuring, and the associated yield response of hops harvested in the following summer.

(a) Period 1948-1953 : K_1, 200 lb. per acre total K_2O x — — — — — x
K_2, 400 lb. per acre total K_2O x————————x
Yield response to K_2 treatment ■ +ve

(b) Period 1953-1958 : K_1, 14 tons dung + 3 cwt. muriate of potash per acre x — — — — — x
K_2, 14 tons dung + 6 cwt. muriate of potash per acre x————————x
Yield response to K_2 treatment ■ +ve, □ —ve.

to the dressing of dung, the relatively slow rise in available potassium is not perhaps remarkable. The K_2 plots, however, received some 4 cwt. per acre muriate of potash annually in addition to dung, and the small effect of this extra potash is surprising and suggests marked potash fixation in this soil. A moderate yield response to high potash manuring was obtained in each of the three years 1950-1952, though in no year was the effect significant ; in 1953 the response was negligible.

Changes in available potassium in the second period of the experiment, from 1954 to 1958, are shown in Fig. 2 (b). In this period the rise in available potassium was more pronounced at the higher levels of potash manuring then adopted, but the difference between the K_1 and K_2 plots remained very steady. However, the yield response to the higher level of potash manuring continued to be very small, in both 1954 and 1955, and in 1958 high potash depressed yield appreciably, though not significantly.

Available magnesium. Fig. 3 shows the changes in available magnesium in

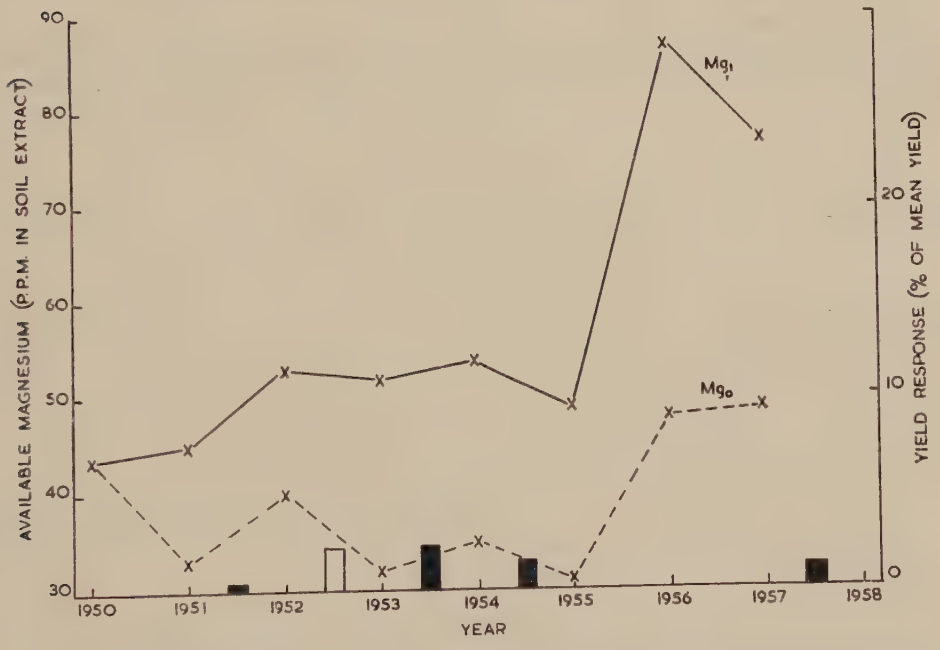

FIG. 3.

Annual increase in soil-available magnesium (sampled mid-winter, 0-6 in. depth) at two levels of magnesium application, and the associated yield response of hops harvested in the following summer.

Period 1950-1958 : Mg_0, 14 tons dung per acre x — — — — — x
Mg_1, 14 tons dung + 5 cwt. Epsom salts per acre x————————x
Yield response to Mg treatment ■ +ve, □ —ve.

the two periods of the experiment. The results show apparent variation from year to year, but it is considered that this is partly related to the analytical method used, since comparable data for exchangeable magnesium on the same samples are more

consistent. The data show that applied magnesium consistently raised the level of available magnesium ($P<0.01$ for each year). With the exception of 1953, there was a small increase in yield with applied magnesium, though in no year was it significant.

Soil analyses—organic carbon and pH.

No significant differences in organic carbon or in soil pH were found with the different manurial treatments, but over the period of the experiment the mean pH rose from 6·4 to 6·9.

Leaf analyses.

The leaf analysis data for the two periods of the experiment are summarized in Table II. All the leaf constituents determined showed higher values in the second period, reflecting the increase in soil fertility as the experiment progressed.

TABLE II.

Effect of manurial treatments on the chemical composition of hop leaves. Mean values for the periods 1951-1953 and 1954-1958, expressed as percentage of dry matter.

Period	Element	Treatment means								Overall mean
		N_1	N_2	P_1	P_2	K_1	K_2	Mg_0	Mg_1	
1951-1953	N	4·69	4·81	4·74	4·76	4·79	4·72	4·76	4·74	4·75
	P	0·49	0·50	0·47	0·52	0·50	0·49	0·50	0·49	0·49
	K	2·41	2·44	2·43	2·42	2·28	2·57	2·46	2·39	2·43
	Mg	0·33	0·35	0·34	0·34	0·36	0·32	0·34	0·35	0·34
	Ca	1·47	1·47	1·42	1·52	1·56	1·38	1·49	1·45	1·47
1954-1958	N	4·94	5·06	4·99	5·01	5·00	5·00	5·01	4·99	5·00
	P	0·51	0·51	0·51	0·51	0·52	0·50	0·51	0·51	0·51
	K	2·69	2·67	2·71	2·65	2·62	2·74	2·72	2·65	2·68
	Mg	0·39	0·40	0·40	0·40	0·40	0·40	0·38	0·42	0·40
	Ca	1·78	1·80	1·78	1·80	1·79	1·79	1·82	1·76	1·79

Nitrogen. Throughout the period of the experiment the higher level of nitrogenous manuring increased leaf nitrogen, but the effect was small and non-significant. The other treatments tested had no appreciable effect.

Phosphorus. Up to 1953, the heavy superphosphate dressings given to the P_2 plots increased leaf phosphorus ($P<0.01$). After 1953, when the P_2 plots received no superphosphate, there was no significant difference in leaf phosphorus between the P_1 and P_2 treatments, indicating that plants on soil at a very high level of available phosphorus took up the same amount of phosphorus as plants receiving 10 cwt. per acre superphosphate annually on soil of lower available phosphorus content. The other treatments tested had no appreciable effect.

Potassium. In the first period of the experiment the higher level of potash manuring increased leaf potassium ($P<0.01$). In the second period leaf potassium values were high on both the K_1 and K_2 plots and the difference, though in favour of the latter, was not significant. The other treatments tested had no significant effects, though applied magnesium consistently depressed leaf potassium.

Magnesium. The increase in leaf magnesium content, with applied magnesium, was very small and non-significant up to 1953, but subsequently the effect became more pronounced and was significant ($P<0.05$). Of the other treatments, high potash depressed leaf magnesium ($P<0.01$) in the first period of the experiment.

Calcium. High phosphate manuring increased leaf calcium ($P<0.05$) in the first period of the experiment, the increase presumably being due to the calcium in the superphosphate used. In the second period, however, when the phosphate treatments were adjusted to give comparable levels of available phosphorus on both the P_1 and P_2 plots, there was no significant difference in leaf calcium. High potash manuring depressed leaf calcium ($P<0.01$) in the first period. There were no other significant treatment effects.

Resin analyses.

Resin content varied considerably from year to year, but the effect of manurial treatments was little influenced by seasonal variations, and only the mean data are presented in Table III.

The overall effects of differential manuring on resin content were small and non-significant, but it may be said that the depression in total soft resins associated with the nitrogen and phosphate treatments, and the increase with high potash, were generally consistent throughout the 8-year period.

TABLE III.

Effect of manurial treatments on the resin content of hop cones. Mean values expressed as percentage of dry matter.

Resins	Treatment means								Mean
	N_1	N_2	P_1	P_2	K_1	K_2	Mg_0	Mg_1	
Total soft resins*	11·60	11·45	11·59	11·46	11·35	11·70	11·58	11·46	11·52
Alpha acids†	4·27	4·27	4·27	4·27	4·21	4·34	4·25	4·29	4·27
Beta fraction†	7·23	7·05	7·20	7·08	7·12	7·16	7·14	7·13	7·14

* Mean values for the 8-year period 1951-1958.

† Mean values for the four years 1951-52 and 1957-58.

INORGANIC PLOTS.

For the first two years of the trial the whole inorganic strip received, per acre, 300 lb. N, 350 lb. P_2O_5 and 300 lb. K_2O, corresponding to the mean level of nutrients applied to the dunged plots. In 1951 it was split into four 18-hill plots, two receiving a high level and two a low level of manuring, corresponding to the $N_2P_2K_2Mg_1$ and the $N_1P_1K_1Mg_0$ treatments applied to the dunged plots in the first period of the experiment to 1953. The inorganic fertilizers used were the same as on the dunged plots. These manurial treatments were continued unchanged after 1953, but those given to the dunged plots were altered, so that the two series of plots were not comparable after this date.

Samples of soil, leaves and cones were taken from the inorganic plots on each

occasion when the dunged plots were sampled. Chemical analyses were subsequently carried out by the methods referred to earlier in this paper.

Results.

As the manurial treatments applied to the inorganic and to the dunged plots were not strictly comparable in the second period of the experiment, only the results for the first period are given, with the exception of the data for soil organic matter.

Yield.

As stated above, two levels of nutrients were applied to the inorganic plots, but the variation in plot yield was large and with only two replicates no consistent or significant differences were found. It is of interest, however, to compare the bulked mean yields for the four inorganic plots with the bulked mean yields for the 32 dunged plots, during the period 1950-1953 ; the results obtained are given in Table IV. It will be seen that in each year the inorganic plots outyielded the dunged plots, but over the four years the mean difference was only 0·4 cwt. dry hops per acre.

Table IV.

Effect of dung and of inorganic fertilizers on yield of dry hops in cwt. per acre.

Treatment	Yearly means				4-year mean
	1950	1951	1952	1953	
Dung plus inorganics ..	11·6	27·8	13·6	13·2	16·6
Inorganics only	12·1	28·0	14·4	13·6	17·0

Soil analysis—available nutrients.

Available phosphorus. Fig. 4 (a) shows the build-up of available phosphorus on the inorganic plots, together with the comparable data for the dunged plots. It is seen that in 1949 and 1950, when the inorganic strip received a uniform dressing of 350 lb. P_2O_5 per acre, the rise in available phosphorus corresponded to that found on the P_1 dunged plots. In the period 1951-53, the build-up of available phosphorus on the P_1 and P_2 inorganic plots, then receiving 200 lb. and 500 lb. P_2O_5 per acre respectively, closely followed that on the comparable P_1 and P_2 dunged plots.

Available potassium. Fig. 4 (b) gives the corresponding build-up of available potassium. The results show that in 1949 and 1950, when 300 lb. K_2O per acre was applied to the whole inorganic strip, the increase in available potassium corresponded to that found on the K_1 dunged plots. In the period 1951-1953, the K_2 inorganic plots, then receiving 400 lb. K_2O per acre, closely followed the comparable K_2 dunged plots in build-up of available potassium, but the K_1 inorganic plots, receiving 200 lb. K_2O per acre, rose above the corresponding K_1 dunged plots.

Available magnesium. The increase in available magnesium on the inorganic plots receiving Epsom salts was similar to that found on the comparable dunged plots (Table V).

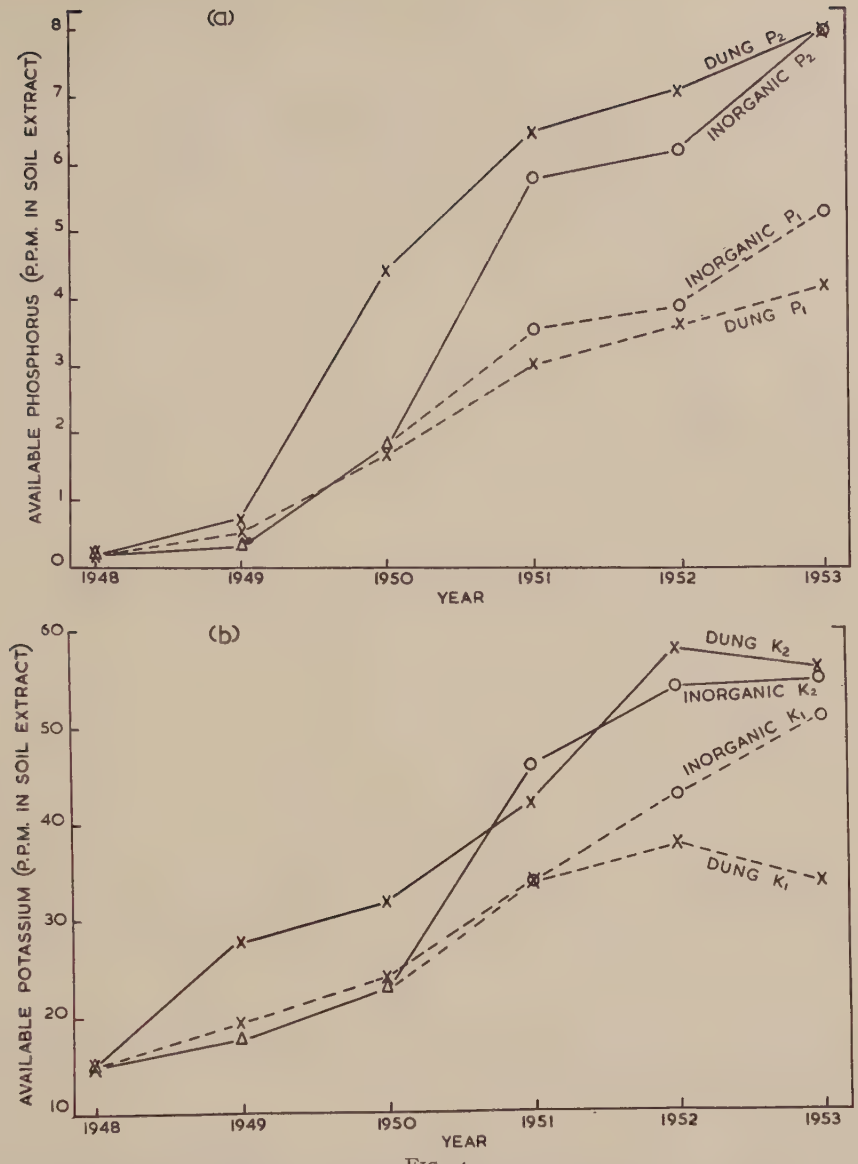

FIG. 4.

Annual increase in soil-available nutrients (sampled mid-winter, 0-6 in. depth) with " dung + inorganics " and " inorganics only " manurial treatments.

(a) Available phosphorus

Dung treatments : (P_1) 200 lb. total P_2O_5 per acre x — — — — — x
(P_2) 500 lb. total P_2O_5 per acre x——————x

Inorganic treatments : (P_1) 200 lb. total P_2O_5 per acre o — — — — — o
350 lb. total P_2O_5 per acre △——————△
(P_2) 500 lb. total P_2O_5 per acre o——————o

(b) Available potassium

Dung treatments : (K_1) 200 lb. total K_2O per acre x — — — — — x
(K_2) 400 lb. total K_2O per acre x——————x

Inorganic treatments : (K_1) 200 lb. total K_2O per acre o — — — — — o
300 lb. total K_2O per acre △——————△
(K_2) 400 lb. total K_2O per acre o——————o

TABLE V.

Effect of dung and of inorganic fertilizers on soil-available magnesium. Mean values for the period 1951-1953, expressed as p.p.m. in soil extract.

Manurial treatment	Magnesium treatment	
	No Mg	55 lb. per acre Mg
Dung plus inorganics ..	35	50
Inorganics only	32	46

Soil analysis—organic carbon.

A summary of the mean values for the inorganic plots for the period 1954-1958, together with comparable data for the dunged plots, is given in Table VI.

TABLE VI.

Effect of dung and of inorganic fertilizers on the percentage organic carbon content of soil (Walkley-Black values).

Manurial treatment	Yearly means					5-year mean
	1954	1955	1956	1957	1958	
Dung plus inorganics ..	1·65	1·70	1·71	1·86	1·88	1·76
Inorganics only	1·56	1·54	1·60	1·80	1·63	1·63

On the inorganic plots, with the exception of 1957 when the value was unaccountably high, there was little change in the organic carbon content of the soil. On the dunged plots the organic carbon rose steadily from 1954 to 1958, and was consistently higher than on the inorganic plots ; this increase in organic matter was associated with a better soil structure than was found on the inorganic plots.

Leaf analyses.

A summary of the results obtained from the inorganic plots, together with the corresponding data for the dunged plots, is given in Table VII.

TABLE VII.

Effect of dung and of inorganic fertilizers on the chemical composition of hop leaves. Mean values for the period 1951-1953, expressed as percentage of dry matter.

Element	Treatment			
	Dung + inorganics		Inorganics only	
	$N_1P_1K_1Mg_0$	$N_2P_2K_2Mg_1$	$N_1P_1K_1Mg_0$	$N_2P_2K_2Mg_1$
N	4·69	4·81	4·81	5·02
P	0·47	0·52	0·49	0·52
K	2·28	2·57	2·44	2·51
Mg	0·34	0·35	0·35	0·41

Nitrogen. In both series of plots the higher level of nitrogen increased leaf nitrogen, but the effect was more marked on the inorganic plots.

Phosphorus. Leaf phosphorus values were similar, and showed a comparable increase with high phosphate manuring on both the dunged and inorganic plots.

Potassium. The higher level of potash increased leaf potassium in both series of plots, the effect being more pronounced on the dunged plots.

Magnesium. Applied magnesium increased leaf magnesium on the inorganic plots but not on the dunged plots, an effect for which there is no obvious explanation.

Resin analyses.

Table VIII summarizes the results obtained from the inorganic plots and the corresponding data for the dunged plots. On the former the differences associated with the high and low levels of nutrition were small and inconsistent, and only the overall mean values are given.

The results show that resins were consistently higher on the inorganic than on the dunged plots.

TABLE VIII.

Effect of dung and of inorganic fertilizers on the resin content of hop cones. Mean values expressed as percentage of dry matter.

Resins	Year	Treatment	
		Dung + inorganics	Inorganics only
Total soft resins ..	1951	11·59	12·09
	1952	9·91	10·21
	1953	12·00	12·57
Alpha acids	1951	4·07	4·24
	1952	3·16	3·28
Beta fraction	1951	7·52	7·85
	1952	6·75	6·93

DISCUSSION.

On a soil initially of low fertility, receiving a basic annual dressing of dung, differential manuring with inorganic fertilizers over a 10-year period influenced hop yield, and produced significant differences in the levels of available phosphorus, potassium and magnesium in the soil, as measured by a quick extraction method using Morgan's reagent.

The yield response to nitrogen manuring was inconsistent, though in general high nitrogen tended to depress yield, particularly in years favouring vigorous growth. Under such conditions, although cropping potential is large, excess nitrogen may encourage vegetative growth at the expense of cone production.

The yield responses to phosphate and potash manuring were related to the levels of available phosphorus and potassium in the soil, which at the beginning of the trial were in the " very low " categories. With phosphate, in the first year of harvesting (1950), the response to the extra 300 lb. P_2O_5 per acre applied to the high phosphate plots was a 25% increase on mean yield but, as the level of available phosphorus rose on the plots receiving the standard phosphate manuring, the yield

response dropped in each successive year, falling to 7·6% in 1953. In this year the soil on the high phosphate plots reached the " very high " category, and subsequently these plots received no phosphate other than that contained in an annual dressing of dung, but nevertheless continued to outyield the standard phosphate plots for the next two years. In 1958, however, when the levels of available phosphorus on both series of plots were comparable, the yields were virtually the same.

With potash, the yield response to the extra 200 lb. K_2O per acre applied to the high potash plots was an increase of some 8% on mean yield in each of the three years 1950-1952, during which period the level of available potassium on the plots receiving standard potash manuring rose to the " medium-high " category. Subsequently the yield response to high potash fell to some 2% and in 1958, when available potassium on the standard potash plots had reached the " very high " category, the extra potash given to the high potash plots depressed yield by 8%. The reasons for this depression are not obvious, but it is possible that it was associated with interaction effects between potassium and magnesium, since the response to high potash was generally lower in the presence of magnesium.

The response to magnesium applied as 5 cwt. of Epsom salts per acre was an increase in yield in five out of the six years for which data are available. With the exception of 1952, however, the response was very small (under 5% increase on mean yield) although applied magnesium significantly increased the available magnesium in the soil throughout the period of the experiment. High potash manuring tended to depress yield response to magnesium.

In this experiment leaf analysis did not prove to be a very sensitive indicator of yield response to differential manuring. The higher levels of NPK and Mg tested generally resulted in a higher leaf content of the corresponding nutrient, but in some instances this was associated with a depression in crop yield—the well-known phenomenon of luxury consumption. The absence of unmanured plots in this trial makes it impossible to assess threshold values for leaf nutrients but, compared with data obtained from Fuggle hops in mineral deficiency plots (Thompson, 1959), the leaf nutrient values were always above deficiency levels. It is likely that this was due initially to the nutrient reserves in the cuttings planted, and to the subsequent generous manuring given to the plots, even with the lower level treatments. It is, however, of interest that in the first period of the experiment, when yield response to high potash was at a maximum, leaf potassium was significantly higher on the K_2 plots, whereas in the second period, when the response to high potash was slight or negative, there was no significant difference in leaf potassium between the K_1 and K_2 plots. It is also noteworthy that it was only in the second period of the experiment that leaf magnesium was significantly higher on the Mg_1 plots, and only in this period that any increase in yield was obtained from applied magnesium.

With regard to hop resins, Thompson and Burgess (1952) suggested, from preliminary work, that manuring had little influence on the resin content of Fuggle hops. Later work by Keller and Magee (1954), in the U.S.A., supported these findings with Fuggle hops, but with Oregon Cluster, a variety of much higher resin content, they found that high nitrogen depressed resins and high potash increased resins, both effects being significant. In the present experiment similar trends were found with the Fuggle variety, although differential manuring produced no statistically significant effects on resin content. A further point of interest is that complete inorganic manuring had no deleterious effect on resin production, although it is fre-

quently maintained that organic manuring enhances hop quality, in which resin content is an important factor.

The bulked mean yield on the plots receiving dung plus inorganic fertilizers was consistently lower than on plots supplied with the same total quantities of nutrients per acre from inorganic fertilizers only. The yield difference, however, was small (0·4 cwt. dry hops per acre), implying that, with a perennial crop like the hop, the nutrients in dung can become available to the plant over a period of years. This conclusion is supported by the fact that the available nutrients in the soil increased at comparable rates on both the dunged and inorganic plots. On the other hand, the dung applications increased soil organic matter and improved soil structure, and the influence of these factors on root development and nutrient uptake cannot be overlooked. Whatever the explanation, however, it is apparent that, with the hop, the manurial value of dung should be assessed higher than is customary with annual crops.

Although it has been shown that, in terms of yield and resin production, hops can grow satisfactorily for a number of years with inorganic fertilizers only, the consequent loss of organic matter and deterioration of soil structure can lead to difficulties in soil management in hop gardens. In consequence, it is desirable that any manurial scheme for hops should be based on regular applications of organic matter, preferably as dung.

On this basis, Burgess's (1949) recommendation of 75 to 150 lb. of mineral nitrogen per acre, plus the nitrogen in a 15-ton-per-acre dressing of dung, which he assessed at some 175 lb. per acre, may be taken as a suitable dressing for hops, the precise amount being governed by seasonal conditions, in the absence of a satisfactory method for determining the available nitrogen in the soil. Burgess's recommendations for phosphate and potash manuring, however, should be reconsidered in relation to soil analysis data, since it is evident that, at very high levels of available phosphorus and potassium, there may be little or no response in yield to fertilizer applications. In practice, the soils in established hop gardens frequently contain very high levels of these available nutrients and there is a strong case for applying no inorganic phosphate or potash fertilizers to such soils, where dung is used. On soils low in available phosphorus and potassium, however, and particularly where a field is newly planted to hops, very heavy applications of phosphate and potash can be justified, with the object of building up the available nutrients to medium-high to high levels as rapidly as possible. Subsequently the aim should be to maintain these levels by relatively small annual applications of inorganic fertilizers and regular dressings of dung, but more information is needed before specific recommendations can be made as to the rates of manuring required to achieve such conditions, though preliminary results obtained from recently established factorial NPK trials (Thompson, unpublished) suggest that quantities of the order of 70 lb. per acre of both P_2O_5 and K_2O may be adequate.

Soil analysis can also be of importance in assessing the magnesium requirements of the hop plant, particularly in view of the antagonism between magnesium and potassium and other ions. Very low levels of available magnesium are uncommon in hop garden soils, but induced magnesium deficiency has been reported by Thompson *et. al.* (1950) on a soil of satisfactory magnesium status but very high in available potassium. In the present trial, though symptoms of magnesium deficiency were infrequent and never severe, the yield response to applied magnesium was greater at

the lower level of potash manuring, emphasizing that with the Fuggle hop heavy potash manuring should be avoided where the level of available potassium is very high.

The use of soil analysis data as a basis for manurial recommendations has been criticized in recent years, and there is little doubt that to attempt precise recommendations on such a basis can be misleading. With a perennial plant like the hop, however, where cultural practices change little and soil conditions remain reasonably uniform from year to year, the possibilities of relating manuring to soil analysis are greater than with land under mixed arable cropping. The results of this trial have encouraged the establishment of more extensive manurial experiments on a range of soil types, to serve as calibration trials.

SUMMARY.

1. A long-term factorial manurial experiment with hops, variety Fuggle, on land initially of low fertility, is described. Two levels of N, P, K and Mg manuring were tested on plots receiving a basic annual dressing of dung. The experiment also provided a broad comparison between "dung+inorganics" and "inorganics only" treatments.

2. Manurial treatments had significant effects on crop yield and on the levels of available phosphorus, potassium and magnesium in the soil, as measured by a quick extraction method using Morgan's reagent.

3. In general, high nitrogen tended to depress yield. With high phosphate and high potash, yield response was large initially, but decreased as the levels of soil-available phosphorus and potassium rose to the "very high" category, in both treatments, after which the response became very small or negative. Applied magnesium increased soil-available magnesium significantly, but had only a small effect on yield.

4. Leaf analysis was not a very sensitive indicator of yield response to differential manuring in this experiment. Leaf nutrients, although increased by the higher levels of manuring tested, were initially above deficiency levels with all treatments.

5. Differential manuring had no marked effect on hop resins, but high potash tended to increase, and high nitrogen to depress, the resin content of the cones.

6. There was no appreciable difference in yield response between an "inorganics only" manurial treatment and one of "dung+inorganics" calculated to supply the same total quantities of N, P, K and Mg. Dung had no beneficial effect on resin content but increased soil organic matter and improved soil structure.

7. It is recommended that hop manuring should be based on regular applications of dung supplemented by annual top dressings of mineral nitrogen. The need for supplementary dressings of inorganic phosphate and potash fertilizers should be assessed in relation to the level of available phosphorus and potassium in the soil.

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THE USE OF DEFOLIATING SPRAYS FOR THE CONTROL OF BIENNIAL BEARING IN APPLE

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Considerable success in the control of biennial bearing in apples has been achieved in America and some other countries by the use of blossom-thinning sprays, but in England such sprays have given inconsistent or unsatisfactory results. Since chemical thinning in the " on " year has so far proved unreliable, attention has been turned to possible " off " year treatments which, by affecting the tree at a time when fruit buds are initiated, might lessen the number of fruit buds formed. Defoliation is such a treatment.

Singh (1948a, 1948b) reviewed earlier literature on the effect of defoliation on fruit bud formation and began investigations into the value of defoliation in the " off " year as a control for biennial bearing. He found that a severe defoliation by hand was necessary to produce a noticeable reduction in the number of fruit buds formed and that, whereas early in the season it did not reduce blossom formation appreciably, it was effective about four weeks later. He also experimented with different chemical defoliants. These results were confirmed and extended by Davies (1952), who obtained a significant reduction in fruit bud formation and some improvement in regularity of bearing of biennial trees of the variety Bramley's Seedling by using a 2% copper sulphate spray as a defoliant.

Thus both the degree of defoliation and the time of treatment in the season appeared to be important factors in determining the success of this method as a control measure. The two trials reported in this paper were carried out to obtain more information about these factors. Several concentrations of copper sulphate were used as defoliant sprays and were applied at different times in the season. The amount of scorching of the leaves which developed within five days of applying the sprays was assessed by Dr. Llewelyn of this Station and will be described by him elsewhere ; an account is given here of the subsequent behaviour of the trees throughout the following seasons.

TRIAL I.

Materials and methods.

This was carried out in 1955 in a large orchard at Manor Farm, Icklesham, Sussex, on a south-facing slope a few miles from the sea. The trees were eight-year-old Laxton's Superb apples on M.II, cropping biennially and fully " off " in 1955, interplanted with Worcester Pearmain as pollinators.

Thirty trees were used, divided into six blocks of five treatments. These were $1\frac{1}{2}\%$, 3% and $4\frac{1}{2}\%$ copper sulphate, and two untreated controls. Since the principal comparisons were to be between the treatments and controls, the comparison was improved by including extra controls.

The sprays were applied hydraulically with a hand lance, using a coarse droplet size and low pressure to minimize drifting. The trees were sprayed to run off as evenly as possible, each tree receiving about 3 gallons. The solutions were made up with commercial grade copper sulphate, and Agral LN was added as a wetter at 0·1%.

The treatments were applied on 15th June 1955, approximately 3 weeks after the average time of full bloom for this variety and locality, at a stage corresponding as nearly as possible to that used in the earlier trials (Davies, 1952). The weather was cloudy, warm and humid, with a slight breeze.

Results.

Spray damage to leaves.

Heavy scorching was observed on the trees within 1-2 hours after spraying, and by the end of the day the treated trees looked brown. Five days later all the sprayed leaves showed large necrotic areas, the 1½% treatment causing a little less than the others ; but scorching was uneven over the trees and this was most noticeable in the weakest spray. The percentage of total leaf area scorched, as determined from samples of leaves from the trees, was 0, 46·9, 57·5 and 62·7 for controls, 1½%, 3% and 4½% copper sulphate sprayed, respectively. Differences between the three spray treatments were small, the amount of scorch being severe on all.

New growth.

In the 1½% and 3% treatments, damaged leaves in which the necrotic areas of the leaves were not extensive abscissed within 2-3 weeks after spraying. The 4½% spray killed not only the lamina of the leaves but also the abscission layer, for many dead leaves were still attached to the spurs four months later. New growth from spur terminal buds, which had already begun to form by the time the spray was applied, and from axillary buds on maiden wood that had not been killed by the sprays, followed defoliation and produced a good cover of foliage by autumn. These new leaves did not appear to be smaller than those on untreated trees, and in 1956 leaf size was bigger on the treated trees, even when treated trees with no crop were compared with untreated trees in an " off " phase.

Shoot growth.

A certain amount of green unripe wood was killed back about three or four inches by the 3% and 4½% sprays ; some two-year wood was killed by the 4½% spray, but the total amount of dead wood weighed only a few pounds per tree and was about a quarter of the weight of wood normally removed in pruning. It was not necessary to prune the sprayed trees in the winter following treatment, other than to remove the dead wood. This was because the new shoot growth which developed after treatment was much reduced, about 6 in. long on the average, and was mostly lateral growth, whereas control trees had formed many laterals and leaders of 24-30 in.

Blossoming.

The amount of blossom recorded in the year following treatment and in subsequent seasons is shown in Table I.

TABLE I.

Estimated percentage of spurs blossoming in following seasons on Laxton's Superb sprayed with defoliant sprays in 1955.

Year	Control	Copper sulphate sprays (%)		
		1½	3	4½
1956	92	60	32	20
1957	0	68	80	90
1958	100	30	5	5
1959	0	85	98	100

The treatments all reduced the amount of blossom in 1956 and, as a result, the sprayed trees carried a crop of flowers in 1957, when the control trees were in their "off" phase. But the amount of blossom in 1958 was only about half or much less than half of that in 1956 and, with the "on" crop of flowers in 1959, it would seem that the trees were reverting to a biennial bearing habit, though now out-of-step with the unsprayed trees.

Blossoming in 1956 on treated trees was uneven; in a large branch system with 60% of the possible flowering spurs in blossom there were small branches which were entirely vegetative. This was true of large areas of the tree also, some areas having only a thin scattering of flower clusters while others were relatively profusely covered in bloom. There was no suggestion that these areas were correlated with aspect.

Cropping.

Details of the crop obtained for each treatment in the first two years after the sprays were applied are set out in Table II.

The total crop for the two-year period was increased by the treatments, both in weight of crop and in number of fruits, though in the 1½% treatment this was not

TABLE II.

Cropping of trees sprayed with defoliant sprays in 1955.

Year	Total crop weight (lb. per tree)				Total no. of fruits per tree			
	Control	Copper sulphate sprays (%)			Control	Copper sulphate sprays (%)		
		1½	3	4½		1½	3	4½
1956	292	172	120	64	1,278	700	417	201
1957	3	224	340	372	15	839	1,265	1,472
Total*	304	388	456	420	1,293	1,539	1,682	1,674
L.S.D. from control at P=0·05		104	88	88		361	307	307

* Adjusted by girth.

significantly different from the controls because of the large variation among the trees. It is noteworthy that, despite the presence of a part crop in 1956, the trees in the 3% and 4½% treatments carried a crop in 1957 at least as great as the " on "-year control trees did in 1956.

The treatments made the trees more regular in habit and this is shown clearly in Table III where the data are expressed in terms of the index (I) of biennial bearing.*

TABLE III.

Effect of defoliation treatments upon intensity of biennial bearing for years 1956-1957 ; treatments applied in 1955.

Index of biennial bearing			
Control	Copper sulphate sprays (%)		
	1½	3	4½
0·97	0·33	0·47	0·75
L.S.D. from control at P=0·05	0·23	0·20	0·20

The most even cropping was obtained from the 1½% treatment, although this was not significantly different from the 3% treatment. The 4½% spray tended to reduce the crop too much in the first year and so reversed the phase of bearing ; hence the difference between the value of the index for this treatment and that for the controls was only barely significant.

At harvest the picked fruits were graded by diameter and the data analysed statistically. The mean fruit size on sprayed trees was greater than that on control trees (Table IV), but there were no significant differences in diameter between the spray treatments.

TABLE IV.

Mean fruit diameter (in.) on trees treated with defoliant sprays ; treatments applied in 1955.

Year	Control	Copper sulphate sprays (%)		
		1½	3	4½
1956	2·68	2·83	2·83	2·87
1957	(no crop)	2·98	2·94	2·93

TRIAL II.

MATERIALS AND METHODS.

This trial was done in 1957 in an orchard at Broadstreet Farm about two miles away from the earlier trial, and lay on the NE side of a small valley a little farther

* This index is found by dividing the difference between the crops of each consecutive pair of years by their sum. Thus a figure o means that crops were equal, a figure 1 that there was no crop at all in the " off " year. The smaller the index the more uniform the cropping. (Hoblyn *et al.*, 1936).

inland than Manor Farm. The trees were ten-year-old Laxton's Superb, in biennial bearing, in an " off " year in 1957, and interplanted with Worcester Pearmain as pollinators.

There were six blocks with eight trees in each. The treatments used were three concentrations of spray at two times of application ; two trees in each block were untreated controls as in the earlier trial. The concentrations used were ¾%, 1½% and 3%, the first of these being chosen because, in the light of the results from Trial I, the effect of the weaker sprays promised to be of greater interest. The two times of application, referred to hereafter as L and E and written after the concentration of the spray applied at that time (e.g. 1½E), corresponded to the timing used in Trial I, i.e. 30th May (L), and ten days earlier (E).

The sprays were made up from commercial grade copper sulphate as before ; 0·1% Agral LN was used as a wetter for the early spraying (E), but 0·02% Aerosol OT with the later one (L). The method of application was the same as in Trial I.

On 20th May the weather was cool and cloudy with a slight breeze from the SW. Ten days later it was mild and cloudy, a light breeze blowing from the SE.

Results.

Spray damage.

No marked signs of scorch were visible when spraying was finished on 20th May and even three days later the scorch was much less than in the previous trial. The 3E spray produced much less scorch than the weakest spray used in Trial I (1½%) and showed the greatest variation in the amount of scorch between trees within a treatment. Scorch from the ¾E spray was negligible (Table V).

Scorch records taken on 3rd June on L trees showed that the damage to the leaves was more severe than it was on E trees at a similar stage (Table V), and on the 1½% and 3% trees many of the leaves had half or more of the lamina dry and curled up. Some trees showed a marked variation from branch to branch in the amount of scorch present—some branches having lightly damaged leaves, whilst on others the leaves were all dead.

Table V.

Percentage of total leaf area scorched following spraying with copper sulphate.

Early spray (%)			Late spray (%)		
¾	1½	3	¾	1½	3
1·3	5·2	19·8	22·1	38·4	52·8

Some defoliation of the sprayed trees was observed two to three weeks later, in some instances spread unevenly over the trees. A similar effect was observed by Davies (1952). Some of the fallen leaves appeared to have little scorch and were a healthy green colour and turgid. Similar leaves on the trees were quite firmly attached. An estimate of the amount of defoliation was made on 17th June 1957 and is summarized in Table VI. It will be seen that there was more defoliation after late spraying and that the stronger the spray the more the defoliation, and this is confirmed by statistical analysis.

Table VI.

Estimated percentage of defoliation following treatment by defoliant sprays.

Early spray (%)			Late spray (%)		
¾	1½	3	¾	1½	3
16	27	74	58	91	95

Shoot growth.

As in the previous trial, the 4½% spray killed back young green shoots to the suberized wood and growth continued from an axillary bud below the dead region. In these treatments some spurs on older wood were also killed. While rather more laterals were formed than on untreated trees as a result of some spurs being forced out into shoot growth, there was a reduction in the number of leaders which was proportional to the strength of the treatment, being very severe in the 3L trees (about 80%). The average length of both laterals and leaders was also reduced by the treatments and again the 3L treatment had the most severe effect, reducing them by 50% and 90% respectively. As before, the total amount of dead wood per tree was very small and much less than that removed by normal winter pruning.

Blossoming.

The amount and stage of development of the blossom was recorded in May 1958 and is summarized in Table VII.

Table VII.

Estimated percentage and stage of development in the following seasons of spurs blossoming on Laxton's Superb sprayed with defoliant sprays in 1957.

	Control	Early spray (%)			Late spray (%)		
		¾	1½	3	¾	1½	3
% of spurs blossoming							
1958	100	90	90	62	90	30	0
1959	0	25	30	49	40	100	95
Stage of development (% fully open on 14.5.58)	75	33	13	3	7	Pink bud	Pink bud

Some reduction in the numbers of fruit buds formed was achieved by the 3E spray, and this treatment produced the most regular production of blossom over the two years 1958 and 1959. The extremes of possible effects of the sprays are shown by the late treatments, the ¾% spray having no significant effect whereas the 3% spray completely reversed the phase of bearing. Flowering in 1958 was later on all the treated trees than on the controls.

DISCUSSION.

Initially the effect of the treatments was upon the leaves and the green unsuberized wood ; subsequently changes occurred in the cropping behaviour of the trees. The bulk of the crop of these trees was carried on spur growth, and therefore

in this discussion the effect of the sprays upon shoot growth has been ignored. A detailed analysis of the development of the spur terminal buds following application of these treatments has been made and will be published elsewhere, but the salient points are mentioned here where relevant.

To appreciate the mode of action of the sprays on bud growth, and hence on cropping, it is necessary to bear in mind how a bud normally develops on an " off "-year tree and what happens when all the foliage leaves are removed. A description of a spur terminal bud was published by Bijhouwer (1924). Briefly the bud consists of a number of leaf primordia surrounding the apical growing point ; below these are transition leaves and finally budscales. The terminal bud itself is surrounded by the foliage leaves which emerge in spring. As the season advances, more primordia are formed by the apical growing point and more budscales are formed from the older leaf primordia. At some time in July induction occurs, and shortly afterwards flower primordia begin to develop in the axils of leaf primordia at the upper nodes ; ultimately the apical growing point itself gives rise to the king flower. If the foliage leaves are removed before induction has occurred, these processes are arrested and the leaf primordia within the bud grow out into a new flush of leaves. Eventually a new terminal bud is formed distal to the new foliage leaves, and this may or may not develop into a flower bud before end of the season.

In Trial II the sprays achieved a degree of defoliation of the trees which was related to the strength of spray used and the time at which it was applied (Table VI). This was only broadly related to the amount of measured scorch (Table V) since leaves which had fallen were observed to be less scorched than those remaining on the trees. Following the treatments, all the spurs on sprayed trees burst into a second flush of foliage except on some of the $\frac{3}{4}$E and $1\frac{1}{2}$E trees, but even on these the spurs had formed more nodes by the end of the season than on the controls.

When the spurs from the 3L trees, which were virtually all vegetative in 1958, were compared with the other treatments it was found that the principal difference was in the distribution of growth, i.e. in number of nodes of the final terminal bud (Z) and of the flushes of leaves, etc., preceding it (Y) (Fig. 1). In the 3L trees there were fewer nodes in the terminal bud than in other treatments and more nodes in Y. This relationship between Y and Z is shown graphically, for all treatments, in Fig. 2. The correlation between Y and Z is $-0{\cdot}77$ ($P=0{\cdot}001$). The slope of the regression is greater than $1{\cdot}0$ because the effect of increasing the severity of the treatment was not only to alter the distribution of growth between Y and Z, but also to increase the total number of nodes (Y+Z).

There was also a sharp change from the vegetative to the floral condition as the number of nodes in the terminal bud increased from 17 to 19 (Table VIII). The

TABLE VIII.

Relationship between the number of nodes in the terminal spur bud (Z) and the % frequency of occurrence of fruit buds.

No. of nodes in Z	15	16	17	18	19	20	21	22	23	24
Total no. of buds	6	12	25	26	41	38	32	24	16	17
% fruit buds	0	0	12·0	38·4	82·9	97·4	100	100	100	100
Theoretical values from probit analysis	0	0·8	9·8	42·3	81·7	97·7	100	100	100	100

relationship between the percentage of buds which were fruit buds, expressed as probit units, and the number of nodes in the terminal bud (Z), was found to approximate to a straight line, and the theoretical values calculated from this line are also shown in Table VIII. In view of the good fit obtained by probit analysis, it follows that if Z is less than 18 the probability of a bud becoming a fruit bud is very small, whereas if it exceeds 18 the probability is very high. Therefore 18 could be regarded as a " critical value " *for the conditions of Trial II*. Under other conditions, however,

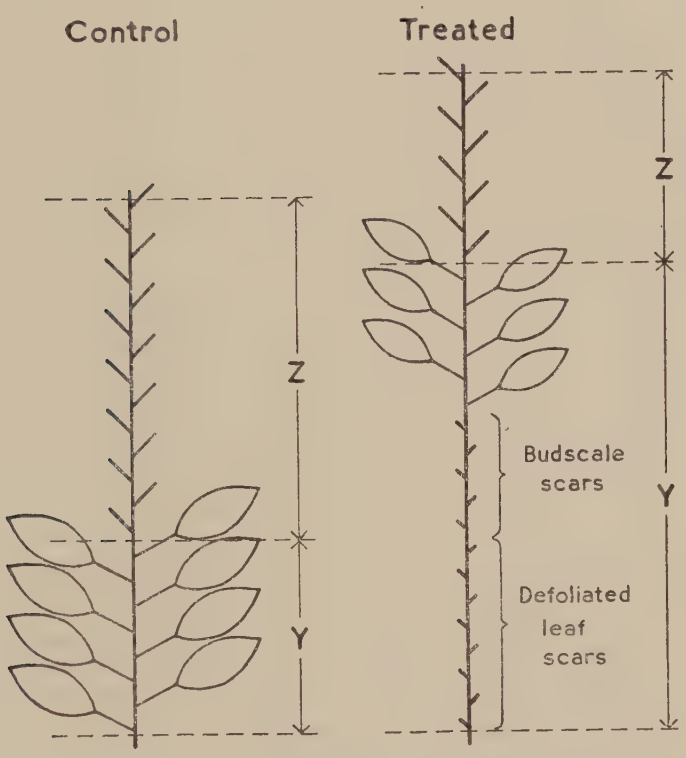

Fig. 1.
The regions of growth referred to by Y and Z.

such as in the late summer blossoms which are frequently found in Laxton's Superb apple, fruit buds with a value of Z much less than 18 may be found. The critical value of Z in this trial is therefore not equivalent to the " minimal leaf number " required to achieve a condition of " ripeness to flower ", as in winter rye and other plants (Purvis, 1934).

As the treatment increased the value of Y, so the mean number of nodes in the terminal bud (Z) fell and approached the " critical value " (Fig. 2). The natural variation about the mean value of Z when it was close to the critical value would result in some of the buds having fewer nodes than 18, and these would tend to remain vegetative. The actual proportion would depend both upon the proximity

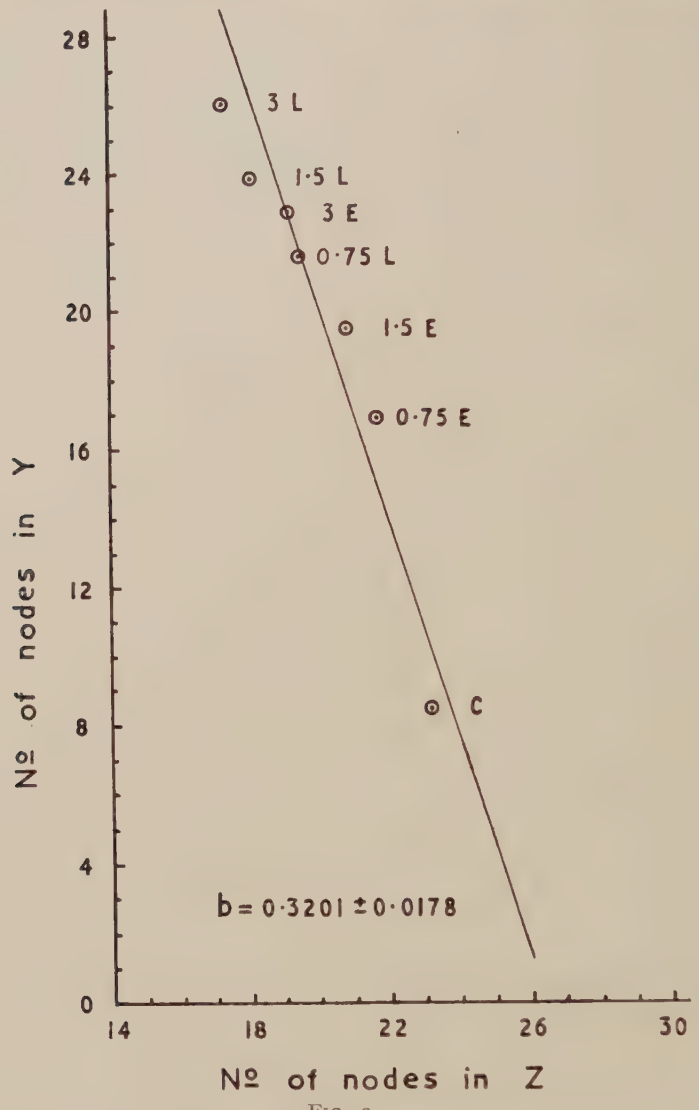

Fig. 2.

Relationship of the number of nodes in the final terminal bud (Z) of spur shoot to the number of nodes preceding it (Y). L, sprayed late ; E, sprayed early ; C, control. Figures on graph give concentration (%) of copper sulphate used.

of the mean value of Z to 18, and also upon the degree of natural variability of the spurs on the trees. There was no evidence to suggest that in Trial II the treatments had altered this variability, but such differences might exist between different orchards, or conceivably between different seasons. With such a sharp change in the proportion of fruit buds near the " critical value ", small differences could result in big effects in terms of numbers of flowering or vegetative

spurs. It is interesting to note that in the treatments where the blossom in the year after treatment was reduced in amount, e.g. 3E or 1½L, the flowers were not distributed evenly over the trees but were in large patches which could not be readily correlated with differences in leaf scorch or defoliation. It suggests that variation in bud growth within localized regions of the tree may be less than over the whole.

As the value of Y increased, so the development of the new terminal bud was delayed and its ultimate size progressively diminished, those buds below a critical size remaining vegetative. Since in other conditions fruit buds much smaller than this critical size are found, the absence of flower formation in the small buds was most probably related to the time when the new terminal buds began to develop, that is to the duration of Y.

The value of Y which results from a treatment is therefore of cardinal importance because of its effect on Z (Fig. 2), and the relationship of the treatments in Trial II to the recorded value of Y is shown in Fig. 3. Since the defoliation produced by the 3L spray was virtually complete, it seems probable that this spray produced almost the maximum effect possible for this time of treatment. Therefore, though the relationship between Y and the strength of spray used was linear over the range examined, it may in fact have been curvilinear and, for higher values of concentration, Y would have reached an asymptotic value very quickly.

The optimal spray treatment for regular cropping in Trial I was 1½% (Table III) and in Trial II it was probably between 1½L and 3E (Table VII), i.e. Y=22·8 to 23·8. A strong spray applied late increased the value of Y too much and, as a consequence, the final terminal bud was smaller than the critical size. These trees were thereby put into an "off" phase for a second successive year. Thus both the correct timing and the strength of spray are important in achieving regular cropping, which is not surprising in view of the sharp change-over from vegetative to fruit buds as bud size increases (Table VIII).

The value of the "near miss" to the optimal treatment should, however, not be overlooked. The total crop over the first two years of the trees treated with 3% and 4½% in Trial I was greater than on the controls, it was spread to some degree over both years, and the fruits were of good size in each year. At Broadstreet (Trial II) it is noteworthy that the ¾E and 1½E trees, which carried a full crop in the first year after treatment equal to that of the control trees, nevertheless formed blossom for the second year equivalent to 30% of the controls. This is the more noteworthy when it is remembered that all these flowers were formed later in the season than on the control trees, viz. after the second flush of foliage leaves; later work, at present unpublished, suggests that such flowers formed after a second flush of growth may set better. It may be that fewer clusters on the ¾E trees are needed to produce a crop equivalent to the controls, so leaving more spurs free of fruit to form fruit buds for the following year. But the crop was spread evenly over these trees, and these fruits lacked the effect which the same number and weight of control fruits had in preventing the formation of fruit bud at all. This effect could allow a greater range in timing, or in strength of spray to be used, than could be tolerated if the aim was to produce regular cropping, even though the effects of the treatment would not last beyond two years after treatment (Table I).

In the next series of trials the differences between orchards and between seasons are being studied, and further attention is being paid to the setting of flowers and formation of fruit bud in the year following treatment. More information on timing

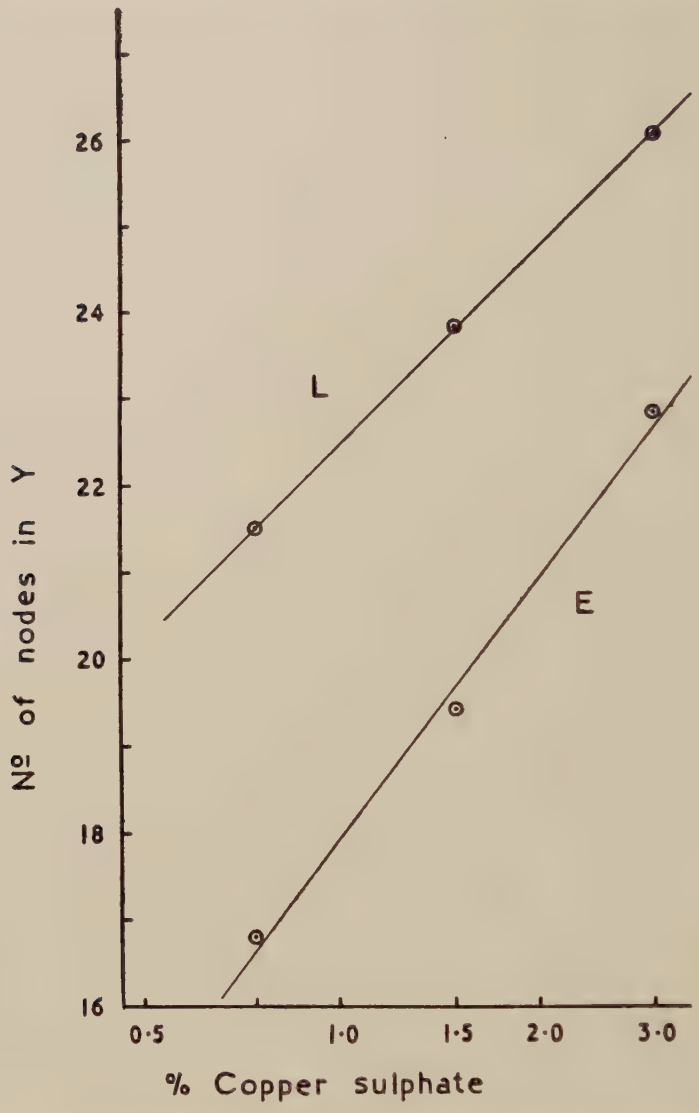

FIG. 3.

Effect of treatment upon the number of nodes (Y) preceding the final terminal bud ; treatments plotted on log scale. L, sprayed late ; E, sprayed early.

of treatments in relation to blossoming or stage of bud development, and on the variation in time of onset of dormancy from season to season, must also be obtained before a full analysis of this technique is possible.

So far there have been four successful trials using this technique, in which more regular cropping has been achieved and no long-term deleterious effects have been observed. In one other trial in which the trees were growing in badly drained soil,

sparse leafing out, stunted leaves and dying back of spurs were observed in subsequent years. In all these trials treatments have only been applied in one season, but there seems no immediate reason why the treatment should not be repeated when necessary in later seasons. In view of the fact that cherry orchards are safely sprayed with copper sprays several times a year it seems unlikely that difficulties would be incurred due to a build up of copper in the soil.

SUMMARY.

Trees of Laxton's Superb apple treated with 1½% copper sulphate defoliating sprays applied in the " off " year, at a time equivalent to three weeks after full bloom, gave more regular cropping than untreated trees for two to three years without further treatment. Both timing and strength of spray to achieve regular bearing were critical, but even the less successful treatments gave an improvement over controls. These results are discussed in relation to the growth and development of spur buds.

ACKNOWLEDGMENTS.

The author gratefully acknowledges the interest and help given by Mr. J. Merricks of Icklesham, Sussex, in whose orchards the trials were carried out. Valuable help was also given by Mr. W. S. English of the N.A.A.S. and the author is indebted to Mr. Jolly, formerly of the Statistics Section of East Malling Research Station, who devised methods of statistical analysis for some of the data. The author would also like to thank Dr. W. S. Rogers for his help in preparing the paper, and his colleague Dr. F. M. W. Llewelyn for his help in field recording. Mr. P. Sprent and Mr. J. Thompson gave much helpful advice on statistical treatment of the data.

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EFFECTS OF ENVIRONMENT ON *RUBUS IDAEUS* L.

V. DORMANCY AND FLOWERING OF THE MATURE SHOOT

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THE initiation of flowers and development of the inflorescence in raspberry plants growing in the field have been described in an earlier paper of this series (Williams, 1959c). The present paper describes a series of experiments carried out in growth rooms to assess the influence of environmental factors upon flower initiation, subsequent development of the inflorescence, and the relation between dormancy, flower initiation and age of the shoot.

In most of these experiments, which were conducted in the glasshouse and growth rooms previously described (Williams, 1959b), plants of the variety Malling Promise were propagated from root cuttings and grown in long days until each shoot had at least twenty nodes above soil level. Preliminary experiments had shown that shoots at this stage were physiologically mature enough to give the responses associated with early autumn conditions in shoots grown out of doors.

RESULTS.

Flower initiation in Malling Promise.

To assess the possible influence of length of day and temperature upon flower initiation, 300 plants were grown in the heated glasshouse to the 20-node stage and then moved to a series of growth rooms under the following conditions :

No. of plants	*Temperature*	*Day-length*
50 } 50 }	60°F. ± 2° (15·5°C.)	{ 16 hour 9 hour
50 } 50 }	55°F. ± 2° (12·8°C.)	{ 16 hour 9 hour
50 } 50 }	50°F. ± 2° (10°C.)	{ 16 hour 9 hour

Two plants were taken from each treatment at weekly intervals and terminal and axillary buds sectioned for evidence of flower initiation. Flower initiation did not occur in either day-length at 60°F., although the rate of elongation of the shoot declined in the shorter days. At 55°F. and in 16-hour days no flowers were initiated, but in 9-hour days flower initials were found in terminal buds after six weeks and thereafter in axillary buds towards the apex of the shoot. At 50°F. flowers were

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initiated rapidly in both day-lengths, the earliest evidence of initiation being found in terminal buds in the short-day treatment after only three weeks (Fig. 1).

Development and growth of fruiting laterals in Malling Promise.

Several plants grown at 50°F. and 9-hour day-length for long enough to bring about flower initiation were then returned to a heated glasshouse under conditions conducive to growth. Most of the buds remained dormant for long periods or, where they started to grow, developed erratically and produced few fruiting laterals. All the buds of some plants were still dormant after eight months. In the field, mature shoots experience a period of low temperatures in winter and early spring after

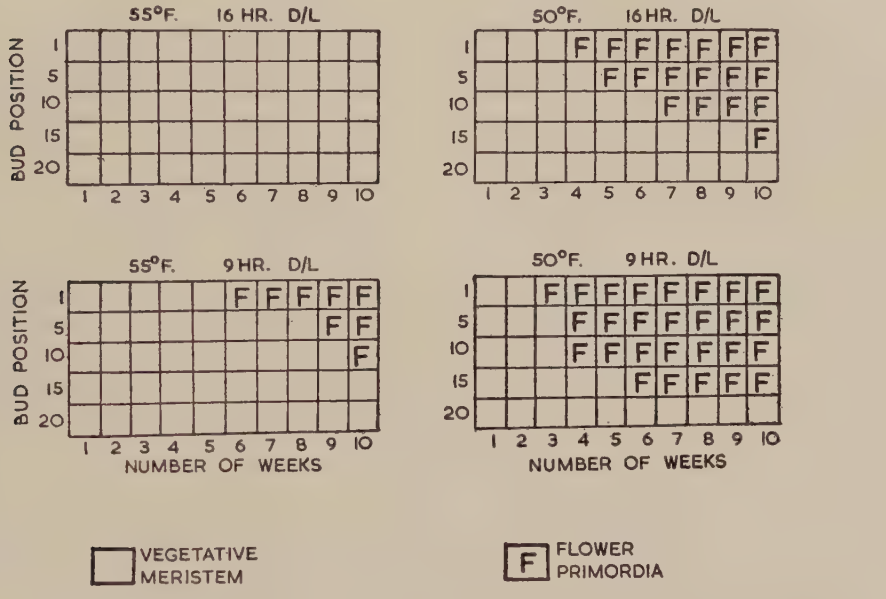

FIG. 1.

Flower initiation in buds of Malling Promise under different conditions of temperature and day-length. Each vertical column shows the position of buds examined from the terminal (No. 1) downwards.

flowers have been initiated, and the effect of low temperature upon subsequent development of flower buds was therefore examined to study the conditions under which dormancy could be broken.

A batch of plants was grown in the heated glasshouse in long days to the 20-node stage and then placed in a growth room at 50°F. and a 9-hour day-length (henceforth described as the " inductive treatment "). At weekly intervals, 25 plants were moved to an unlit refrigerator maintained at 38°F. (the " low temperature treatment ") for a period of six weeks, after which they were returned to the heated glasshouse. In addition, 25 plants were given the inductive treatment and then returned direct to the glasshouse, 25 were given only the low temperature treatment and

25 remained throughout in the heated glasshouse to act as controls. The results are given in Table I.

TABLE I.

Flower initiation under controlled conditions, var. Malling Promise.

No. of nodes above soil level prior to inductive treatment (av. of 25 plants)	Weeks at 50°F. in 9-hr. days	Weeks at 38°F., no light	Number of plants out of 25 which:		Mean no. of fruits per plant
			developed fruiting laterals	developed a terminal inflorescence	
19·8	0	6	0	0	0
20·1	1	6	0	0	0
19·4	2	6	2	3	14
19·9	3	6	4	16	20
20·4	4	6	18	25	20
20·8	5	6	25	25	22
20·3	6	6	25	25	34
20·1	7	6	25	25	25
20·1	13	0	2	0	5

Plants given six weeks of low temperature treatment without inductive treatment failed to develop any fruiting laterals. The tips of many of the shoots were killed, some almost to ground level, and it was evident that a move from a glasshouse at the beginning of August to the low temperature without a period of intermediate hardening conditions was too severe. Plants given thirteen weeks of inductive treatment but no low temperature treatment remained dormant for a number of weeks when returned to the glasshouse (Fig. 2, d), after which some buds elongated at erratic intervals and developed into fruiting laterals.

After one week of inductive treatment followed by six weeks at low temperature, vegetative elongation of the terminal shoot was resumed after plants were returned to the glasshouse. In addition a few apparently vegetative laterals developed from axillary buds but these stopped growing when a few centimetres long (Fig. 2, a). After two weeks' inductive treatment the terminal bud of some shoots developed into an inflorescence, the first instance of " tip fruiting " with this variety in the present work (Fig. 2, b). After three weeks' inductive treatment plants developed terminal inflorescences and some fruiting laterals (Fig. 2, c). Plants which received up to five weeks of inductive treatment produced increasing numbers of fruiting laterals and bud break was rapid, in contrast to plants which had not received the low temperature treatment. Green tips of expanding leaves were frequently visible within twenty-four hours after plants were returned to the glasshouse and development to the fruiting stage was also fairly rapid. For example, a group of plants given inductive treatment from 2nd August to 13th September, then low temperature treatment from 13th September to 25th October, had developed ripe fruit by late December in the glasshouse.

Once flowers had been initiated and dormancy broken, subsequent development of buds to the fruiting stage seemed to be little affected by day-length. In this and subsequent experiments, fruit ripened at all times of the year under the natural length of day prevailing when plants were returned to a heated glasshouse after

appropriate treatments in the growth rooms. Although each plant had about twenty nodes, rarely more than six fruiting laterals developed, even after the longest inductive and low temperature treatments, which suggests that factors other than environment regulate the number of fruiting laterals which a plant of specific size will develop.

Flower initiation and age of shoot in Malling Promise.

It was noted that the environmental conditions which induced and broke dormancy of buds on older shoots were similar to those which controlled the behaviour of emergent root suckers (Williams, 1959b), with the essential difference that flower initiation also occurred during the dormant period in the older shoots. Similarly, in the field, only mature shoots initiate flowers in the autumn, and flowers are not produced in terminal or axillary buds of the short shoots which result from the growth of root suckers in the autumn ; these resume vegetative growth after the period of winter dormancy (Williams, 1959a). It is evident that the flowering response is associated with age of the shoot as well as with environmental conditions, and an experiment was designed to study the " ageing " factor in regard to flower initiation.

Batches of 50 plants grown in the glasshouse under long days were given inductive treatment when the elongating shoot had developed 5, 15 and 20 nodes. A batch of 30-node plants, each more than 150 cm. high, was similarly treated but only 25 could be accommodated because of their size. Plants were removed from each batch at weekly intervals, given six weeks' low temperature treatment to break dormancy, and then returned to the glasshouse to study the effect of increasing periods of inductive treatment on shoots at different stages of development. These results are shown diagrammatically in Fig. 3.

Shoots of all 5-node plants resumed vegetative growth when returned to the glasshouse and earlier groups of the 15-node batch behaved similarly, but after five weeks' inductive treatment a few plants in this group developed terminal inflorescences and thereafter an increasing proportion did so, though some remained vegetative in all treatments. In the 15-node group some plants receiving longer inductive treatment developed one or two small fruiting laterals towards the apex of the shoot (Fig. 4, a). The variability in response of this group suggests that shoots become capable of developing flower initials only at about the 15-node stage under the conditions of these experiments. Plants at the 20-node stage behaved in a similar manner to those described in the previous experiment. Terminal inflorescences developed in some cases after two weeks' inductive treatment and thereafter, up to the fifth week, an increasing number of fruiting laterals developed in addition to terminal inflorescences. At the 30-node stage, rather unexpectedly, plants which had received only one week's inductive treatment developed both terminal and lateral inflorescences (Fig. 4, b). A subsequent experiment showed that, at this age, a period of six weeks at 38°F., without light, was sufficient both to cause flower initiation and to break dormancy of the buds.

Tip fruiting in vars. Lloyd George and Malling Promise.

The previous experiment showed that, with Malling Promise, the induction period required for flower initiation decreases as the shoot ages until even a short period of low temperature without light is effective. In the field, flower initials

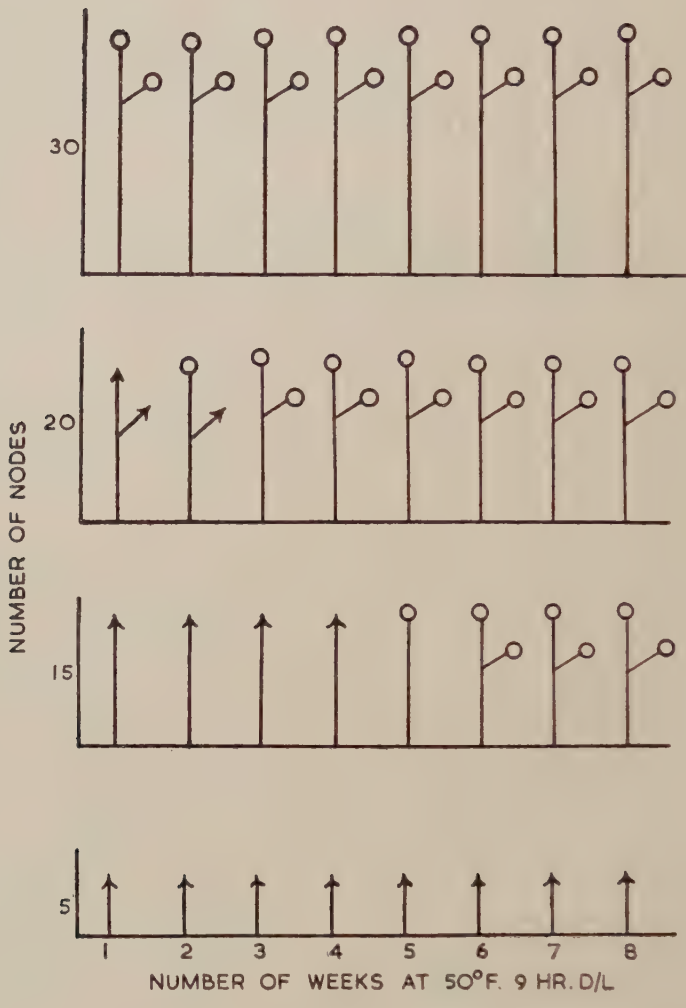

Fig. 3.

Relation between age of shoot and length of inductive treatment in Malling Promise. The length of inductive treatment is shown on the horizontal axis. After the inductive treatment plants in each group were given 6 weeks at 38°F. (no light). Numbers on the vertical axis show the stage of growth of the shoot prior to treatment and symbols show the behaviour of plants when returned to the heated glasshouse as follows : *arrows*, vegetative growth, apical or lateral, resumed ; *circles*, inflorescences, apical or lateral, developed.

were found in the terminal buds of Lloyd George in late July and early August. This suggested that shoots allowed to make continuous vegetative growth would ultimately produce terminal flowers.

To study this point, plants of both varieties were propagated in early February and grown in a heated glasshouse in a day-length of 16 hours (natural day extended by the use of high pressure mercury vapour lamps). During the period from late

PLATE I.

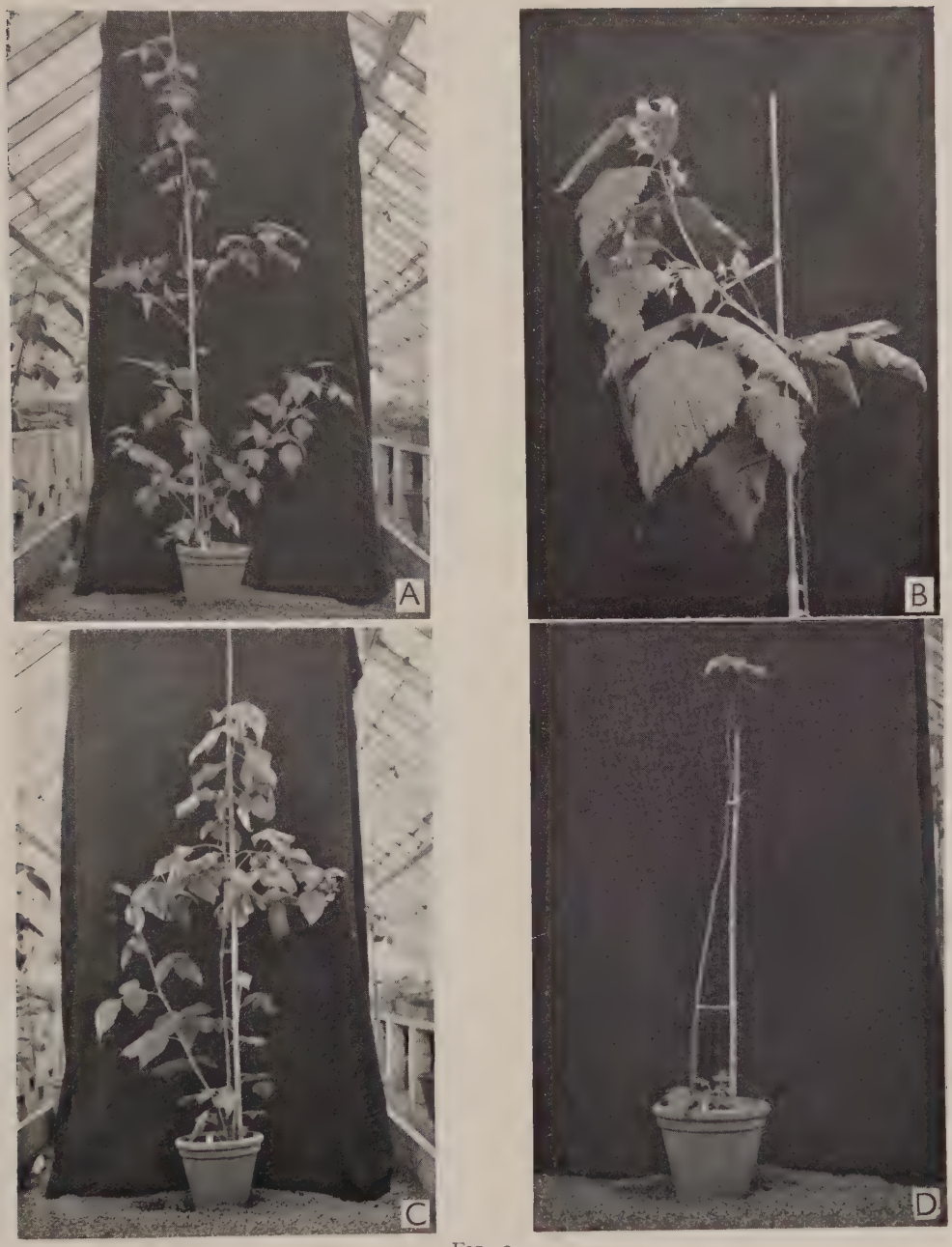

Fig. 2.

Effect of various periods at 50°F. and 9-hour day-length, followed by 6 weeks at 38°F., on the flowering of terminal and lateral shoots of Malling Promise. All plants were at the 20-node stage when treated.

A, After 1 week of inductive treatment, followed by 6 weeks of low temperature, the terminal meristem resumed vegetative elongation and some vegetative laterals developed.
B, After 2 weeks of inductive treatment the plant developed a terminal inflorescence.
C, After 3 weeks of inductive treatment an increasing number of flowering laterals developed.
D, Where no low temperature treatment followed the inductive treatment, buds remained dormant for long periods.

[*face p. 218*

FIG. 4.

Relation between age of shoot and flowering response in Malling Promise.

A. A terminal inflorescence and one fruiting lateral on a 15-node plant after 7 weeks' inductive treatment.

B. A 30-node plant which developed fruiting laterals and a terminal inflorescence after 6 weeks at 38°F. without light, and without a previous inductive treatment.

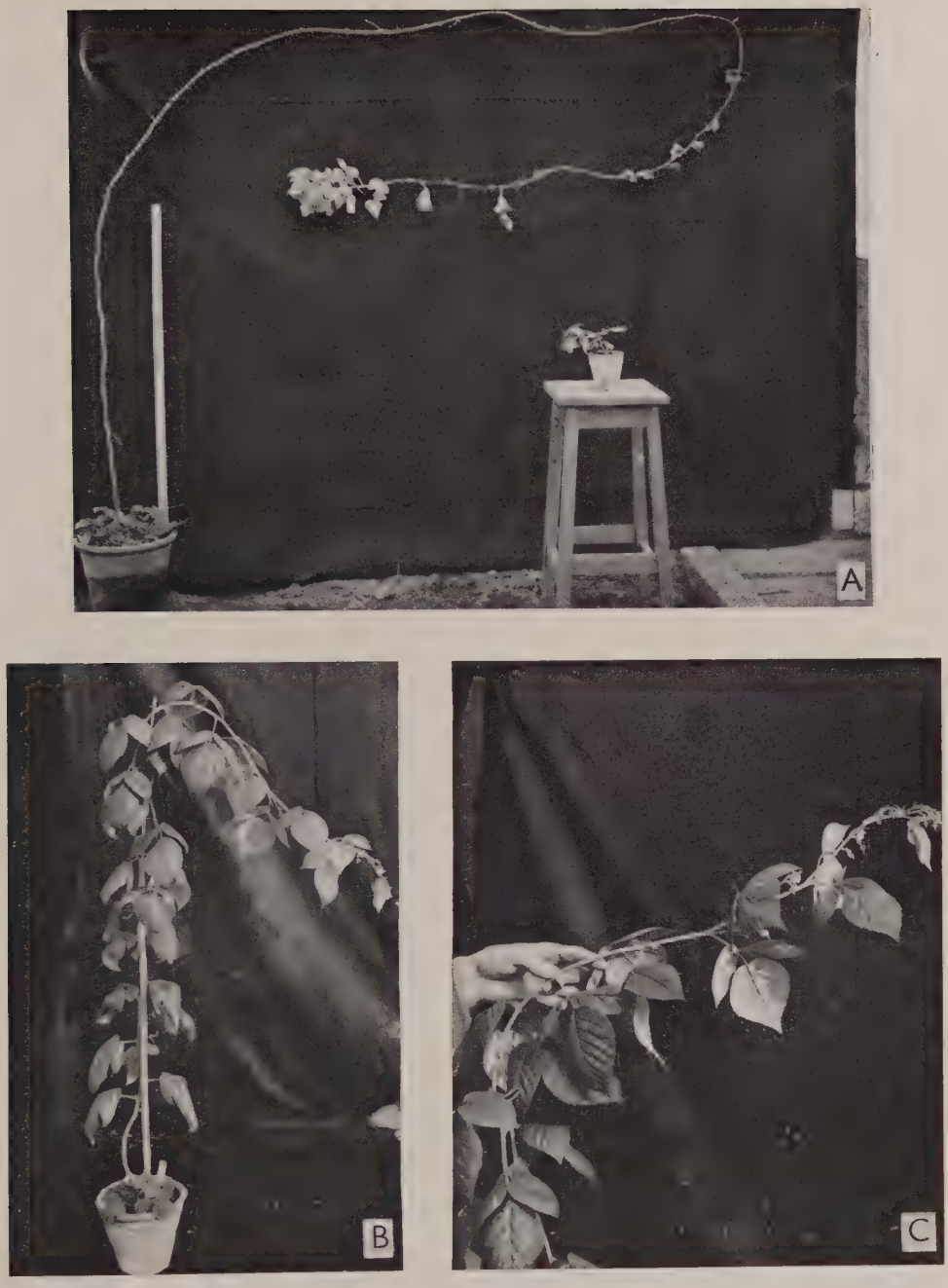

FIG. 5.

The vegetative phase in Malling Promise and Lloyd George raspberries.

A. One of a group of Malling Promise going dormant after having been maintained in a state of vegetative elongation for 19 months.

B. A plant of Lloyd George which, grown under the same conditions, initiated a terminal inflorescence after eight months of vegetative growth.

C. Detail of terminal inflorescence.

August to early October plants of Lloyd George developed terminal inflorescences (Fig. 5, b and c) but vegetative elongation of Malling Promise shoots continued and twelve of these plants were moved into a growth room in which it was possible to maintain a temperature of 60°F. and a light period of 16 hours throughout the winter. In late March the shoots were still elongating and were then returned to the glasshouse where they were trained horizontally below the ridge in such a way that the terminal portions were growing about two feet below the lamps. By September these plants, which had been successively potted on, had vegetative shoots between 18 and 23 feet long and it became impossible to keep them any longer in the glasshouse (Fig. 5, a). Six were moved into the open, allowed to overwinter, then returned to the glasshouse, when they fruited throughout their lengths.

DISCUSSION.

These experiments show that length of day and temperature profoundly affect the major processes concerned in the development of raspberry shoots : namely, their vegetative growth, the initiation of flowers, and the onset and breaking of dormancy. The vegetative phase of the variety Malling Promise can be reduced to a few weeks or prolonged for at least nineteen months. With Lloyd George a similar reduction is possible but terminal flowering meristems were initiated after about seven months of shoot growth even in long days. The relation between flower initiation and dormancy raises the question whether the onset of dormancy is causally connected with the process of flower initiation, or whether the processes must be regarded (as in many other plants) as different responses, in this instance to similar environmental conditions. The results show that the terminal meristems of *young* shoots can pass through a dormant phase without initiating flowers. At the 20-node stage, shoots receiving only a short induction period (50°F. and 9-hour day-length), followed by 6 weeks at 38°F., developed laterals which bore no flowers, suggesting that the dormancy of vegetative axillary buds can also be broken without flower initiation. Flower initiation without dormancy occurred only in the rather special case of the variety Lloyd George, strongly suggesting that, in this instance at least, flower initiation is a separate process.

The partial killing of shoots of Malling Promise moved directly from the glasshouse to a temperature of 38°F. did not occur with plants receiving a short period at the intermediate temperature of 50°F. The importance of this hardening period has been intensively studied in America (Brierley and Landon, 1946, 1954 ; Brierley *et al.*, 1952) and the problem of winter damage in the field was reviewed recently in connection with die-back of fruiting shoots in Scotland (Wood and Robertson, 1957). The techniques used in the present paper could form a basis for controlled experiments on this problem and for considering varietal differences in this respect. Also, the intensive methods of propagation essential to this type of experimentation are finding application where rapid build-up of virus-free stock is needed (Williams and Hudson, 1956 ; Wood, 1959).

SUMMARY.

Studies under controlled environments have shown that day-length and temperature largely control the biennial fruiting habit of shoots of Malling Promise raspberry. The age of the shoot modifies the flowering response since shoots with fewer than

about 15 nodes fail to initiate flowers even under the longest inductive treatment. Conversely, the vegetative phase can be prolonged for at least nineteen months. This is not so with Lloyd George, which develops a terminal inflorescence after about six months' vegetative development even under non-inductive conditions.

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THE USE OF A NEW TECHNIQUE IN BREEDING FOR SOLIDITY IN RADISH

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By sowing radish seed at intervals of 10 to 21 days, with or without the protection of glass, the grower is able to market crops throughout the year. During periods of reduced demand, however, the crop is apt to be harvested at a late stage of maturity when many of the roots are pithy. Because of this uncertainty in time of marketing, there is a need for the production of varieties whose roots remain solid over an extended period.

Krickl (1956) has attempted to produce such a variety by selecting roots which have the least pithiness, as shown when a wedge is removed from mature roots. Lines derived from these selections were shown to be superior to the parental varieties. The main drawback to this method, however, is the time needed to make selections, and a more rapid technique, involving specific gravity, has been used at Wellesbourne.

Method of selection.

It was assumed that the difference between solid and pithy roots would be reflected by a lowering of the specific gravity of the latter. In order to test this assumption, eight varieties of radish were grown, pulled when mature, defoliated just above the crown, and immersed in water. The numbers which floated and which sank were recorded, each root being subsequently cut in half and recorded as pithy, intermediate, or solid, on visual evidence.

The results in Table I indicate that selections of solid roots should be made

TABLE I.

Relation between specific gravity of radish roots and pithiness of flesh.

Variety and type	Sinking roots			Slowly rising roots			Floating roots		
	Solid	Inter-mediate	Pithy	Solid	Inter-mediate	Pithy	Solid	Inter-mediate	Pithy
Cherry (red globe)	5	3	0	8	7	0	0	4	81
Brilliant (red globe)	9	1	3	2	16	1	1	16	85
Gefion Nr. 203 (red-and-white globe)	21	0	0	13	8	0	4	13	113
Carters' 16 Days (red-and-white globe)	1	0	0	2	7	0	0	3	94
French Breakfast (red-and-white intermediate)	22	4	0	5	2	2	0	4	22
White Icicle (long white)	45	7	0	0	9	6	0	0	33
Early Frame (long red)	25	4	1	0	12	2	0	3	55
Early Scarlet Frame (long red)	13	1	0	1	2	0	0	0	7
Totals	141	20	4	31	63	11	5	43	490

from those which sink upon immersion. Roots which do not sink should be discarded.

Immersion tests of commercial varieties and progenies of selected plants.

In order to assess the quality of commercial varieties, 31 red globe, 11 red-and-white globe, 17 red-and-white intermediate, 4 long white, and 6 long red types of radish were grown. In addition, progenies of 6 pair-crosses between selected plants within the red globe (Harrison's Cherry), red-and-white intermediate (Hurst's French Breakfast Forcing), and long red types (Fidler's Early Scarlet Frame) were grown. The respective parent plants were selected for solidity of their roots by the immersion method.

Radishes are normally cross-pollinated and varieties are maintained by mass-pollination of selected plants in the open. Any plant is likely to be pollinated by a number of others. The pair-cross progenies included in this experiment differed from plants of ordinary varieties only by virtue of the fact that both of their parents were known.

The experiment was laid out in the form of three randomized blocks, each containing 75 single row plots with 15 plants per row. Seed was sown under Dutch lights on 4th November 1957, with four varieties, in rows 6 inches apart, under each light. Three harvests were made at weekly intervals with the object of covering the period during which solid roots became pithy. The first harvest was made as soon as the roots had reached a size slightly smaller than that normally marketed. Five plants were taken at random from each plot at each harvest.

The first harvest of the earliest maturing varieties was made 112 days after sowing. These varieties are listed in Table II, and the mean number of days from sowing to first harvest is also given for each radish type.

TABLE II.

Number of days from sowing to harvest of radish types and varieties.

Earliest maturing varieties (112 days)	Type	Mean for varieties of each type
Round Red Winter (Ohlsen's Enke)	Red globe	122
Brilliant (Fogwill)	Red-and-white globe	120
Early Amager (Ohlsen's Enke)		
Amager Oval Vinter (Otto J. Olson)	Red-and-white intermediate	119
Halvlang Hvidspidset (Daehnfeldt)		
Amager Medellang. Brilliant (Weibull)		
Perfection (Fidler)	Long red	117
Glowing Scarlet (Finney)		
(None very early)	Long white	128

The mean percentage of pithy roots for each type at each harvest is shown in Fig. 1. For the purpose of analysis and graphical presentation the slowly rising roots were regarded as being solid.

The most noticeable feature of the graph is the clear-cut difference between

the results for each colour type. At the first harvest the white varieties showed approximately 20% pithiness, the red varieties 40%, and the red-and-white varieties 60%. The greater tendency to pithiness of the red-and-white radish types was mentioned by Robinson (1905) but, as the first harvest of this experiment was made before maturity, the very high percentage of pithiness was quite remarkable. Although less pithiness was exhibited by the red and the white radish types at first harvest, the amounts were still substantial.

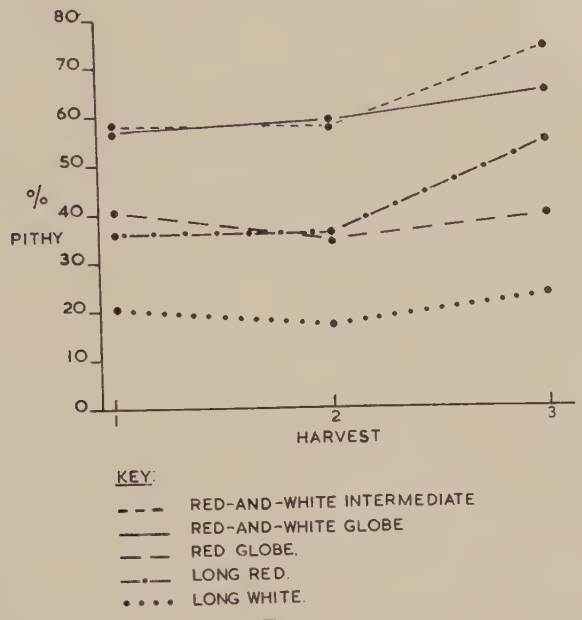

FIG. 1.

Mean percentage of pithy roots for radish types at three dates of harvesting.

None of the radish types showed any appreciable increase in pithiness between first and second harvests, but there was an increase at the third harvest, the greatest amount being shown by the long red and the red-and-white intermediate. These results suggest that the mature roots of radish varieties are able to remain solid for about a week during February and March, although observations at Wellesbourne have shown that the same varieties become pithy much more rapidly when grown later in the year.

Performance of progenies of pair crosses.

The results for the red globe, red-and-white intermediate, and long red varieties are shown again in Fig. 2, where they are compared with those of the respective pair-cross progenies.

All pair-cross progenies exhibited a marked improvement over the commercial varieties at the first harvest. This improvement was maintained throughout by the red-and-white intermediate, not beyond the second harvest by the red globe types, and only for the first harvest by the long red types.

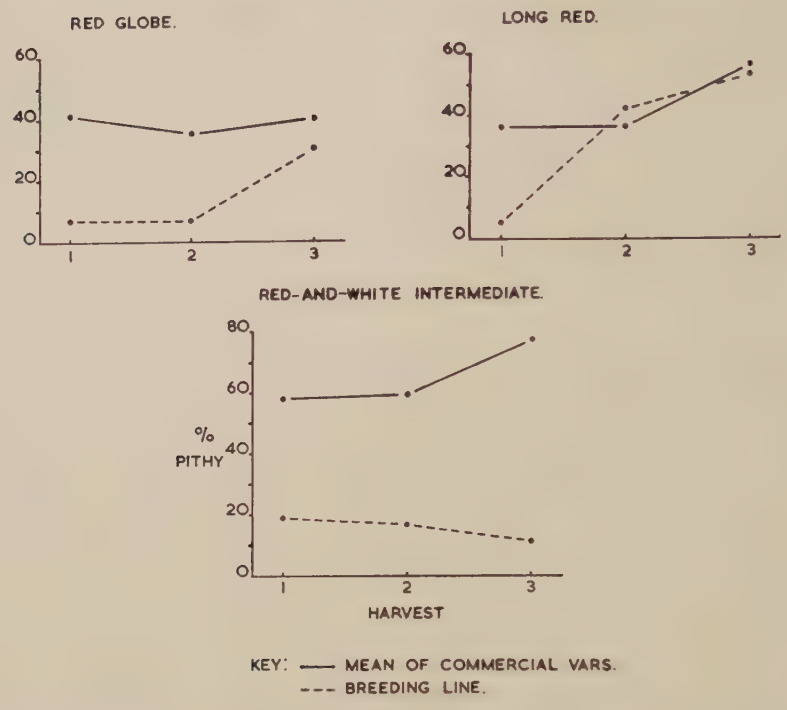

FIG. 2.

Percentage of pithy roots of three radish types at three dates of harvesting ; comparison of breeding lines (pair-cross progenies) with mean of commercial varieties.

No significant differences in the proportion of pithy roots were shown between varieties within the red globe or the long white types over the three harvests. Differences between varieties were significant within the other three radish types, however, and Table III lists the best varieties of each type.

DISCUSSION.

By using the immersion technique it is possible to facilitate the selection of solid roots which will serve as parent plants for the next generation. Its simplicity enables the raising of large seed stocks and of experimental material. The lifting of roots for selection, with removal of the leaves, appears to produce no adverse effects on their subsequent growth ; lifting and transplanting for seed production is actually recommended by Shoemaker (1947) and others. This method should, in fact, facilitate selection for root shape and colour. In our investigations it was noticeable that any solid roots which had been damaged by cabbage root fly larvae also floated to the surface. These unwanted roots were discarded with the pithy ones.

The most surprising result of this experiment was the indication that pithiness occurs in quite a large proportion of the roots before they have reached a marketable size.

TABLE III.

Varieties of radish, arranged according to type, with lowest percentage of pithy roots.

Radish type and variety	Percentage of pithy roots
Red-and-white globe	
Scarlet Gem (Little and Ballantyne) ;	31
significantly better than all except :	
Gaudry (Muller)	47
Red-and-white intermediate	
57050, Pair-cross progeny ex French Breakfast Forcing ;	24
significantly better than all except :	
Half-long Red White Tip (Ohlsen's Enke)	25
French Breakfast 56103 (D. E. S. Saanichton)	40
57045, Pair-cross progeny ex French Breakfast Forcing	44
Tip Top (Harrison)	51
Amager Medellang. Brilliant (Weibull)	56
Frilandssorten (A. B. Gehlins)	56
Long red	
57108, Pair-cross progeny ex Early Scarlet Frame ;	20
significantly better than all except :	
Glowing Scarlet (Finney)	31
Early Frame (Unwin)	33
57040, Pair-cross progeny ex Early Scarlet Frame	36

The progenies of pair-crosses between selected plants showed marked reductions in the amount of pithiness, although the technique had only been used for a single generation. It seems reasonable to expect that this improvement could be maintained by continued selection using this method in further generations.

SUMMARY.

A technique is described, involving the immersion of radish roots in water, which facilitates the selection of solid roots.

Progenies from crosses within varieties between pairs of plants selected by this method were grown in an experiment under Dutch lights, together with 69 commercial varieties. Three harvests were made at weekly intervals, the first occasion being slightly earlier than that at which varieties would normally be marketed, and roots were tested by immersion on each occasion.

There were marked differences in the amounts of pithiness for each of the colour types of the commercial varieties. Approximately 60% of the red-and-white radishes, 40% of the red and 20% of the white were pithy at first harvest. This level of pithiness was maintained for a week, after which it showed a further increase.

The pair-cross progenies showed considerably less pithiness than their parental types, although in the long red types this applied only to the first harvest, and the possibility of producing improvement in the quality of radish varieties by further selections using this technique is indicated.

ACKNOWLEDGMENTS.

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BRITISH PARASITIC FUNGI. By W. C. MOORE (Cambridge University Press. Pp. 430. Price 45s.).

A comprehensive guide to all the parasitic fungi reported on cultivated plants in Great Britain, the diseases which they cause and the British literature on the subject, compiled by the Director of the Ministry of Agriculture, Fisheries & Food Plant Pathology Laboratory, Harpenden, Hertfordshire.

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